

## CHAPTER 6

### POPULATION DYNAMICS

#### 6.1 Introduction

In view of the large stocks of mussels in billabongs of the Magela Creek (Chapter 5) and the very large fraction of the total benthic biomass that these comprise (unpublished determinations), study of the population dynamics of Velezuno angasi was deemed important from the point of view of providing basic information needed to assess the influence of its populations in the energy budgets (via production estimates) of billabongs on the Magela Creek. Growth data, while essential for determining other population parameters (e.g. age structure, mortality) were also needed for proper understanding and determination of structure of the breeding populations. Finally, various population parameters (growth rates, recruitment relationships, mortality rates and age structure) could conceivably provide valuable baseline data upon which to monitor the effects of environmental changes such as potential pollutants. These are further indicator roles in which V. angasi might be employed.

Aspects of the population dynamics of V. angasi undertaken, included age and growth, size and age structure, recruitment, mortality, and movements. Literature reviews appropriate to these studies appear in Appendix 3. While considerable attention has been devoted to the dynamics of freshwater mussel populations in North America and Europe (see Appendix 3), very few comprehensive studies have been carried out on populations of either Australian or tropical freshwater mussel

species. Walker (1981b) studied aspects of the ecology of freshwater mussels in the Murray River in temperate Australia, and Kenmuir (1980) and Dudgeon and Morton (1983) studied tropical species in Zimbabwe and Hong Kong respectively. On both counts therefore, the present study from tropical northern Australia greatly adds to an area lacking in knowledge.

## 6.2 Materials and methods

Quantitative field sampling and later subsampling of mussels in the laboratory for use in determining population parameters have been described earlier (sections 3.3 and 5.2). The method of age determination is described below (section 6.3.2).

The growth of individually marked mussels was monitored at regular intervals in Georgetown, Corndorl, Mudginberri, Island, Leichhardt and Nankeen billabongs. Marks and numbers for later recognition were engraved on the dorsal portion of the left shell, as described in section 3.3. Plastic containers filled with the surrounding billabong sediments were used to hold the mussels. Between 5 and 6 containers were used in each billabong and the density of mussels placed in each container was approximately the same as that prevailing on the surrounding substrates. The containers were filled flush to the rim with sediments and embedded well into the bottom substrates of the billabong. Thus, water circulation around the mussels placed on the surface of the container's sediments was unimpeded and the level at which siphoning occurred was almost the same as those mussels siphoning on the nearby sediments. Fine fishing mesh (2 cm stretched

knot-to-knot) covered the mussels to prevent them moving out of the containers. Containers were placed in waters at depths closely approximating those "preferred" by mussels for the particular billabong (section 5.4.1.1) and were always close to a station that was, or had been used in routine collecting (section 3.1).

In this way, the growth of at least 60 marked mussels in each billabong was monitored at approximately 3 to 4 month intervals over the course of at least an 18 month period. The regular measurements of growth in length, were performed in the field and individual mussels were never out of the containers nor water for more than 15 minutes. Dead mussels were replaced during these occasions.

No inhibition of growth by the handling involved in marking was ever apparent. This was indicated by the fact that newly marked mussels added to the containers from time to time to replace dead mussels, grew at comparable rates at the subsequent inspection and measurement, to mussels of similar size which had been resident in the containers for some time.

In addition to growth rate measurements of mussels made at regular intervals, other measured and marked mussels were scattered free into the surrounding sediments about the containers, remaining undisturbed for later recovery toward the end of the study (April-May, 1982).

A major mark-recapture programme was undertaken in Buffalo billabong to observe the migratory patterns of mussels in deep billabongs over the course of a year. Approximately 8,000 mussels were collected,

marked and individually allocated to, and released over, predetermined gridded portions of the billabong during May 1980. The billabong was gridded by way of 22.5 x 22.5 m quadrats (Fig. 6.39) marked by buoys. Bankside markers ensured that the pattern was exactly repeatable twelve months later when the buoys were reset, and mussels recollected.

The sex of individual mussels was determined according to methods described in section 7.3.

### 6.3 Age determination

#### Background

Study of some of the population parameters of Velesunio angasi such as growth, age structure and mortality, largely depended upon finding a suitable and accurate method of age determination. Three standard methods have been used to determine the growth rate and age of bivalve molluscs (Haskin, 1954): (1) study of length frequency distributions; (2) release and recovery experiments; and (3) use and interpretation of annual growth rings.

For freshwater mussels (as in marine bivalves), analysis of annual cessation rings on the shells is regarded as rapid and efficient, and is by far the most common aging method in population studies. Haukioja and Hakala (1978a) have extensively reviewed the techniques and methodology as they apply to freshwater mussels. In most bivalve populations, the differences in successive modes in size frequency

distributions are of limited use in aging, as generally there are only one or two peaks - adults, or young of the year and adults. Release and recovery studies are also infrequently employed, as an extended period of time is required to produce reliable results and growth between individuals of the same habitat may be highly variable. Nevertheless, in populations of freshwater mussels from the tropics where growth interruption lines have been difficult to interpret, length frequency analysis has been used to age seasonal breeding species (Dudgeon and Morton, 1983), and release and recovery experiments used to determine age and growth rates of continuous breeders (Kenmuir, 1980).

The use of shell rings produced by a cessation of growth, for age determination, is dependent upon confirming their annual or periodic nature. Chamberlain (1931) and Stansbery (1961) and recently McCuaig and Green (1983), reviewed the developmental studies that first described the microstructure of the conspicuous interruption bands which led to ascertaining their annual nature in the shells of freshwater mussels from temperate climates. In short, Coker et al. (1921) showed that doubling-up of outer shell layers was formed by repeated startings and stoppings of growth in late autumn and early spring, giving the appearance of a dark, broad and compound band on the shell. Other disturbance rings were the result of only single duplications of shell while winter rings showed several repetitions. In both earlier and subsequent studies, moreover, a seasonal growth pattern of mussels was shown by Lefevre and Curtis (1910), Isely (1914) and Sebestyen (1942), with growth ceasing over the winter period; and a one-to-one correspondence between successive winters and

added shell annuli during mark-recovery experiments shown by Lefevre and Curtis (1910), Coker et al. (1921), Isely (1931), and Sebestyen (1942).

In temperate regions, false annuli are believed to result from: water shrinkage and drought; rapid temperature fluctuations in summer; summer reproduction; seiches; transport or stranding by floods; pollution; or even tagging and handling (Isely, 1914; Coker et al., 1921; Crowley, 1957; Stansbery, 1961; Negus, 1966; Walker, 1981b; McCuaig and Green, 1983). While true winter annuli are noted to be more heavily marked (Coker et al., 1921, Negus, 1966), other criteria have been drawn up for distinguishing these from other disturbance rings (Chamberlain, 1931; Stansbery, 1961; Tevesz and Carter, 1980b). Nevertheless, some workers have been reticent to use shell annuli as the basis of age determination, while others have expressed caution and suggested that considerable experience might be needed to distinguish true rings (Crowley, 1957; Okland, 1963). The shells of some species are inherently difficult to age as growth lines are ill-defined or closely packed: e.g. Margaritifera margaritifera (Roscoe and Redelings, 1964), Elliptio complanata (Matteson, 1948; Ghent et al., 1978; Strayer et al., 1981) and certain small creek species (van der Schalie and van der Schalie, 1963). Otherwise, the nature of the environment may render some shells more difficult to age than elsewhere. Shells of mussels from lentic environments for example, have notably regular spaced and distinct annuli, and are free of false rings as found in river-dwelling mussels; this has been attributed to the less marked fluctuations in seasonal temperature changes in large bodies of water such as lakes (Brown et al., 1938;

Stansbery, 1961; Tevesz and Carter, 1980a). Finally, Comfort (1957) noted that growth rings provided reliable age estimates, where estimates are confined to species and to localities, and where a fixed and consistent pattern of rings can be confirmed.

#### 6.3.1 Seasonal growth pattern

Having established that distinct rings are present on the shells of mussels, a prior assessment as to their annularity or shorter-term pattern of consistency might be gained from monitoring the sequence of shell growth throughout the course of a year or more (Jones, 1983). While growth of mussels in temperate climates slows down or ceases during winter, droughts and the silt carried by monsoonal floods were suggested by Tevesz and Carter (1980a) as possible factors that might cause growth interruption in mussels from warmer or tropical regions. Late Dry season food depletions were believed by Kenmuir (1980) to slow the growth rates of mussels in Lake Kariba at this time, while growth of Anodonta woodiana, in Plover Cove Reservoir was also retarded in the late summer Dry (Dudgeon and Morton, 1983). Dudgeon and Morton did not suggest causal factors in the growth decline of mussels, but the period is associated with thermal and oxygen stratification of the reservoir while temperatures are at their summer high (c. 23°C).

Growth rates of Velesunio angasi were monitored regularly in a number of billabongs on the Magela Creek (section 6.2). Figure 6.1 shows the pattern of seasonal growth of mussels in representative billabongs, expressed as percentage of the growth completed over an 18 month

period. (Figures 6.5 and 6.6 show the marginal increments of shell growth from the last annulus to the shell edge, monitored monthly in representative billabongs. These may be used to complement the patterns shown in Figure 6.1).

The pattern of growth of mussels inhabiting the braided creek channel above Mudginberri billabong (section 3.1), was not studied. A clear seasonal growth cycle, however, is preordained for these populations. As they are obliged to aestivate over the Dry (Jun.-Nov.), growth can only occur during the Wet and early Dry.

The seasonal growth patterns of mussels in Georgetown and Nankeen billabongs are representative of those in the majority of billabongs on the Magela Creek and are typical of all other backflow billabongs and other floodplain billabongs that become turbid late in the Dry (Coonjimba, Gulungul, Corndorl, Hidden, Ja Ja and Jabiluka). Growth begins with the initial replacement of turbid waters by early Wet season flushing (Dec.-Jan.), is most rapid in the early Dry and continues but steadily declines as waters become turbid again between the mid to late Dry (Fig. 6.1). Apparently growth is related to availability of food which for *V. angasi* comprises unicellular algae and detritus (section 8.3). A partial measure of available food is chlorophyll content of the waters as shown in Figures 2.28 and 2.29. Algal populations are suppressed by increasingly turbid waters (section 2.3.2.5), a factor presumably responsible for growth cessation of mussels during the late Dry.

Growth rates of mussels in Mudginberri and Island billabongs were



highest from the late Wet until the late Dry. During the Wet, growth rates of mussels were low. These billabongs are well, to reasonably well, flushed in the Wet (section 2.3.1.3) and at these times algal populations are stifled. Figures 6.5 and 6.6 further exemplify the pattern in Mudginberri billabong of minimal shell growth during the Wet season. Growth in these billabongs, however, was also suppressed late in the Dry (Fig. 6.1) despite this being a time of high algal productivity in both waterbodies (Figs. 2.28 and 2.29). Algal blooms themselves may be the cause of deterioration in water quality over the late Dry. In addition to causing stressful overnight oxygen depletions, sudden crashes in algal populations that have been observed in at least Island billabong at these times, reduce the available food temporarily, and cause even more general and severe bottom water anoxia (Walker *et al.*, 1983a). A close correspondence is observed between shell growth and relative condition (i.e. body weights) of mussels in the late Dry. In the channel billabongs condition declines in the late Dry (section 8.7.1) when larval production is at its peak (section 7.10.1). Presumably the energy channelled into reproductive effort at this time is at the expense of both shell and somatic growth. Further, other stresses are observed during the late Dry in channel billabongs. Their generally non-turbid nature may impart a stressfully warm environment upon bottom dwelling mussels with the onset of summer (Table 2.6). (Low water temperatures of course, are not factors of importance to growth of mussels in the Region. Lowest water temperatures recorded in the Magela Creek (Table 2.6) are still some 10°C warmer than levels generally reported to induce dormant behaviour in temperate species.)

Mussels in Leichhardt billabong showed the slowest growth rates from the late Wet to mid Dry. This period coincides with a time of often severe oxygen depletions to which this billabong is particularly susceptible (section 2.3.2.2). These periods of hypoxia may suppress metabolic processes including feeding in mussels. This phenomenon may also explain a similar but less marked pattern of growth retardation of mussels in Island during the early Dry, a billabong also notably deficient in oxygen at this time (section 2.3.2.2). The Dry season of 1981 was a particularly severe one in terms of oxygen depletions in Leichhardt (Fig. 2.21), and presumably the growth rates of mussels in this billabong at this time are not always suppressed to the extent shown in Figure 6.1 each and every year. As in the channel billabongs, growth of adult mussels at least, in Leichhardt billabong was also retarded during the late Dry (Fig. 6.1), despite high observed chlorophyll values at these times (Fig. 2.29). The dynamics of algal populations, high reproductive efforts and/or high temperature in the relatively clean waters may explain the reduced growth rates. A further result of stress is the reported kills of a proportion of mussels in Leichhardt billabong with the initial Wet season flushes (section 5.5).

#### 6.3.2 Method of age determination

In the present study, growth interruption rings on the shells were used to age mussels, while length frequency distributions and release and recovery experiments were used in part as checks against, and to validate the aging method. Shells of Velesunio angasi show quite distinct growth interruption rings that in most cases are spaced

regularly and consistently in mussels from the same location. An annual pattern to the rings was most likely given the seasonal nature of the environment and especially after having ascertained clear seasonal growth patterns for mussels in most billabongs. Aging by shell annuli was particularly appealing in view of the rapidity and accuracy with which determinations could be made, especially in consideration of the large numbers of mussels needed to be aged from the quantitative samples.

Strong transmitted light as used by several workers (Chamberlain, 1931; Stansbery, 1961; Coon et al., 1977; Walker, 1981b) greatly assisted the aging method. Placed immediately behind the shell (generally the left valve), the dark growth bands stood out in bold relief against the lighter background of the surrounding, thinner shell material.

The prominent bands on the shells of V. angasi were always obvious and distinct along the postero-lateral axis, and in populations from some shallow backflow billabongs (Gulungul and Corndorl), did not always extend circumferentially to the anterior portion of the valve. Apart from some older shells from Mudginberri and Buffalo billabongs, the appearance of the dark growth bands was highlighted by new and lighter Wet season growth. From confirmatory shell measurements (section 6.3.3.2), these bands were shown to be annular and were laid down during the late Dry season in accordance with the observed seasonal growth patterns.

The usual difficulties as found by most workers (Okland, 1963; Magnin

and Stanczykowska, 1971; Coon et al., 1977; Haukioja and Hakala, 1978a) were experienced in discerning the closely packed annuli of older individuals. These problems were particularly pertinent to the old (> 20 years) and stunted mussels that are commonly found in still, backwater regions of Mudginberri and Buffalo billabongs. A needle-tipped pointer was an aid in these cases, in the often painstaking task of moving outwards along the postero-lateral axis, and separating and counting the crowded annuli. For difficult (old) shells, three age determinations were made. These determinations never varied by more than three and rarely by two years amongst all of the shells aged. A further difficulty in age determinations of older shells was found in individuals from stony sediments (e.g. station 5 in Mudginberri, section 3.1), where the region about the umbo was badly eroded. However, in accordance with the method of Stansbery (1961) who reported similar problems, by knowing the general periodicity of the annuli in the particular environment, and by noting the spacing represented by the remaining annuli on the mussels in question, the number of missing annuli could be estimated. Such eroded shells were uncommon, but in long-lived species such as Margaritifera margaritifera erosion is such a problem in older specimens, that valves are aged by counts of the annual layers in the ligament (Hendelberg, 1960; Bjork, 1962; Stober, 1972; Smith, 1976; Bauer, 1983).

A feature of the shell appearance of juvenile (young-of-year) mussels from non-turbid billabongs (channel billabongs and Leichhardt) was the general absence of a distinct, dark annulus formed at the end of their first Dry season. While growth is continuous throughout the first

year in mussels from these environments, nevertheless, a colour change in the shell was generally discernible between the seasons. Invariably, thicker and darker Dry season shell growth followed by abrupt, thinner (presumably faster) and lighter shell growth accompanied the appearance of the shell between Dry and Wet seasons.

Less prominent, false bands were characteristic of the shells of mussels from floodplain billabongs, particularly Nankeen and Jabiluka. The nature and distinguishing feature of false annuli in the shells of various freshwater mussel species have been reviewed by Chamberlain (1931), Stansbery (1961) and Tevesz and Carter (1980b). Major properties of vagueness, incompleteness, and irregularity are ascribed to false annuli. However, true annuli in shells of individuals from particular environments were also notably incomplete (see above) while the false annuli observed on individuals from floodplain billabongs were often of a regular nature lying between the more prominent true annuli. Nevertheless, while false annuli were generally incomplete, their distinguishable characteristic was their vagueness and thinness. The often regular appearance of the false annuli and their occurrence generally in shells from floodplain environments were strongly indicative that the regular and annual oxygen depletions that occur in these billabongs during the early Dry (section 2.3.2.2) were the cause of the minor interruption to shell growth. A thin and false ring was also a feature of the shells of juvenile (young-of-year) mussels from Mudginberri and Buffalo billabongs. The ring was also traceable to the early Dry season (from back-calculated growth measurements), again suggestive of the sensitivity of juveniles to the even less marked depletions in oxygen (Fig. 2.20) that accompany the

cessation of flow through these billabongs in the early Dry season.

In practice, the annual rings of mussel shells from most billabong environments were not difficult to interpret. Difficulties arose in two environments only, Mudginberri and Buffalo, in which the exact ages of some old mussels were not determinable. However, in view of the small numbers of difficult shells and the careful approach taken to aging these, it is unlikely that these errors alter in any way the appearance of the age structure of the populations of the two billabongs. As expected from the marked seasonality of their environment, the shells of mussels inhabiting the creek channel above Mudginberri were by far the easiest to age. Mussel shells from turbid billabongs also possessed pronounced and easily interpretable annual growth rings. Individuals from Island and Leichhardt billabongs are fast-growing (section 6.4.2) and relatively short-lived (section 6.6.3), factors that ease the interpretation of growth bands considerably as noted by Haukioja and Hakala (1978a) in populations of Anodonta piscinalis. It was notable finally, that the growth bands of shells from Leichhardt were similarly laid down during the late Dry season, so that the stresses that arise then are apparently of more marked effect than early-mid Dry season oxygen depletions that were presumed to have slowed growth of mussels here during the 1981 Dry season.

All shells of mussels subsampled and used for subsequent reproductive and condition studies (section 3.3) were aged.

### 6.3.3 Validation of the aging technique

Graham (1929) listed five separate procedures for testing the validity of age determinations. While these methods have been applied extensively to studies of fish populations, they are nevertheless applicable to any fisheries problem. Growth studies with freshwater mussels are particularly well suited to such analysis. The methods (modified for molluscs) are: the occurrence of discrete length-frequency distributions which correspond with the age determinations; the study of annual, cyclical changes in shell morphology; observations of the progress of dominant year-classes; the recovery of marked individuals after a known interval; and the observation of individuals confined in tanks or ponds. Jones (1983) added that for marine bivalves, while counts of internal bands from sectioned shells were far more accurate than conventional studies on external shell growth patterns, annual shell periodicities either way could be substantiated by monitoring the seasonal growth patterns throughout the course of a year or more, or by using stable or radioactive isotopes to determine growth rates.

Rather than the above methods, Chamberlain (1931), Crowley (1957) and Walker (1981b) argued that the consistency and regularity of the disturbance lines and the uniformity of the growth curves for freshwater mussel populations justified the assumption of their annularity. Walker (1981b) conceded, however, that further substantiation was required. Other authors have effectively argued that in temperate zones, (1) the regularity and clarity of the rings on shells from lake environments; (2) their conspicuous and inherent

nature in shells of particular species (e.g. Anodonta), or (3) previous substantiation of their annularity in either similar environments or in the same species elsewhere, were valid grounds for assuming annularity in the growth bands of the shells in question.

In populations of V. angasi in the Magela Creek, regularly and consistently spaced rings on the shells of individuals from the same environment, and a uniformity of the derived growth curves between populations (section 6.4.2) were observed. Moreover, a seasonal growth pattern of mussels was found that corresponded to shell patterns of alternating seasonal growth and growth cessation. Nevertheless for unequivocal justification of the aging method, it was possible to satisfy three of Graham's (1928) five above criteria for validation completely, and one partially.

#### 6.3.3.1 Length-frequency distributions

Aided by knowledge of the time of impoundment and subsequent colonisation by mussels, Dudgeon and Morton (1983) found year classes of Anodonta woodiana in Plover Cove represented by fairly discrete peaks in the monthly length frequency distributions. Subsequent analysis of the peaks enabled them to age mussels and estimate growth properties of the mussel population. Walker (1981b) also found length frequency distributions of Alathyria jacksoni in the Murray River, useful aids to interpreting the age structure of its populations at various sites along the river. In the Crapina-Jijila marshes, however, Tudorancea (1969) considered length frequency analysis an inefficient aid in growth studies of mussels as distinct modes were



only present for the first two years of life, after which considerable overlap of age classes occurred.

Although seasonal recruitment of V. angasi occurs in billabongs of the Magela Creek, similar observations to those of Tudorancea (1969) were made showing that length frequency distributions were of limited value as progression in the modes of the first two year classes only, could be followed. For the two age classes nevertheless, age as determined by modal peaks corresponded in every case to age as determined by shell annuli, thus partially substantiating the aging method. Figures 6.2-6.4 show the monthly length frequency distribution of mussels collected from Georgetown, Mudginberri and Nankeen billabongs respectively, populations for which quantitative and non-selective sampling was accomplished (section 3.2.1). Two age classes can generally be distinguished as discrete modes, particularly for populations from Georgetown billabong where growth during the first year is not particularly rapid by comparison to populations from Mudginberri and Nankeen. For young-of-year mussels, growth rates from all populations are clearly discernible, as the modes progress through the season to the position previously occupied by the next older age group.

#### 6.3.3.2 Shell morphology

By measuring the distance from the shell margin to the last-formed annulus at regular intervals throughout the season it should be possible to demonstrate the time of annulus formation (and importantly that only one such ring is formed each year), when an abrupt change

occurs at a critical time from relatively wide marginal bands to extremely narrow widths. This method has been used to substantiate age determinations of some marine bivalves (Okera, 1976; Taylor and Venn, 1978) while Negus (1966) used a variation of the technique for validating her age determinations of freshwater mussels in the Thames. By recording the months when winter rings first became visible, Negus was able to demonstrate their time of formation and annular nature.

Monthly measurements of marginal shell increments were made on shells from Georgetown, Mudginberri and Nankeen billabongs for the two year period of the study. Mean values are plotted according to appropriate age divisions, against time of year in Figures 6.5 and 6.6. Marginal increments were standardised for age by multiplying mean values by the mean age of mussels used in the particular age division. In old mussels (> 10 years), a faint transparent edge was found along the shell margins of most individuals during the early Wet, and was interpreted as new shell growth beyond a newly formed annulus. Figures 6.5 and 6.6 clearly show that the marginal bands in shells from all billabongs and age classes reach a maximum in the late Dry (December) but decrease suddenly during January following formation of the new ring. The pattern of ring formation was identical in both years of sampling and between all billabongs, and occurred during the Dry-Wet interchange, thus demonstrating its similar timing and establishing its annual nature in backflow, channel and floodplain environments.

#### 6.3.3.3 Dominant year classes

Haukioja and Hakala (1978a) showed that growth rings in one Finnish population of Anodonta piscinalis were formed annually, as a dominant year class in the population moved its position in the age distribution one step to the right each year.

Dominant year classes were present in many of the mussel populations from billabongs of the Magela Creek. They were especially conspicuous in all of the floodplain billabongs. Figures 6.7 and 6.8 show the age distributions of mussels between years sampled, from populations in a number of billabongs. Clearly, each strong year class appears as a successively older age class in progressive sampling years lending very strong evidence to the assumption that the shell rings are in fact annular.

#### 6.3.3.4 Growth of marked individuals

A number of workers have successfully verified the annular nature of shell annuli of temperate freshwater mussels, from mark and recovery experiments. Mussels are released in the field and upon recovery, the number of rings that have appeared over the elapsed period has been shown to correspond to the number of winters that have passed (Lefevre and Curtis, 1910; Coker et al., 1921; Altnöder, 1926; Isely, 1931; Sebestyen, 1942; Negus, 1966; Ghent et al., 1978; Haukioja and Hakala, 1978a).

Marked mussels in Georgetown, Mudginberri and Nankeen billabongs that

were released around the confined individuals in plastic containers (section 6.2) were recovered after a period encompassing two Wet seasons. Details of the times of release and recovery, lengths at release, recovery and at successive annuli upon recovery, and estimated ages at recovery are shown in Table 6.1. On all shells, a faint but discernible false check due to handling was observed at the length corresponding to the time of release. As expected, for older mussels, no more shell growth was observed between the short period from the time of release until the end of the first Dry season. Nevertheless, on all shells, the added area of growth was divided by two distinct rings representing the periods of growth cessation during the late Dry seasons of 1980 and 1981. While no mussels older than 20 years were recovered, it is conceivable that some difficulties may have been faced in discerning added annuli on their shells, as growth of these individuals, particularly in Mudginberri billabong, is exceedingly slow (section 6.4.2).

Kenmuir (1980) aged mussels in Lake Kariba according to mark recovery data. With age determined by shell annuli for one species, the resulting closeness of the two sets of calculated results suggested to him that the growth cessation lines were in fact true annuli. A comparison of the growth data derived from both mark recovery and shell annuli measurements were also used as an independent check on the accuracy of the latter aging method for Velesunio angasi.

Data from marked mussels placed in containers were used in the analyses. Growth data for only a few individuals spanned the entire study period. Much data, however, was available that covered both

shorter time spans (< 18 months) and different seasons. Gulland (1969) described a method of fitting a growth curve to mark recovery data obtained at unequal time intervals, whereby the instantaneous rate of growth, approximated by  $(\frac{l_2 - l_1}{t_2 - t_1})$  is plotted against the mean length  $(\frac{l_1 + l_2}{2})$ , where  $l_1$  and  $l_2$  are the lengths at times  $t_1$  and  $t_2$  respectively. Analysis of the resulting fitted regression line provides estimates of the constants  $L_\infty$  and  $K$  of the von Bertalanffy growth equation, used to describe the length for age relationship in populations of *V. angasi*, and considered in more detail in section 6.4. Thus, the intercept on the X-axis provides an estimate of  $L_\infty$ , and the slope an estimate of  $-K$ . Instantaneous growth rate is plotted against mean length in Figure 6.9 for mussels in Georgetown, Mudginberri and Nankeen billabongs. If growth across the entire size range of mussels were to conform to the von Bertalanffy growth model, the resulting plots would be linear. Clearly this is not the case, and the youngest age class does not conform. This is examined in greater detail in section 6.4. The relevant point here is that growth data for young-of-year mussels were rejected whenever the von Bertalanffy model was fitted. Using regression lines fitted to growth data of adults, resulting estimates of  $L_\infty$  and  $K$  for a number of billabong populations were derived and compared with estimates calculated from shell annuli data from section 6.4.2 (Table 6.2).

The results indicate the limitations when deriving growth rate data from mark recovery experiments that run over a relatively short period of time. Most of the growth data was obtained during 1981, a year in which chlorophyll values (and hence, presumably food availability) were low in comparison with data from previous years (Walker and

Tyler, 1983b), especially in the floodplain billabongs (Fig. 2.29). Thus it is observed from Table 6.2, that  $L_{\infty}$  values are lower and  $K$  values higher (the two parameters being interrelated, Ricker, 1975) in mark recovery data derived from most of the floodplain billabongs. Nevertheless, estimates of the constants compare reasonably well between the two methods used to estimate growth rate data. Importantly, differences in estimates of the constants (or growth rates) between different billabong populations are constant between both methods. The generally close similarity between the growth parameters derived from both methods is further evidence that shell annuli in Velesunic angasi from billabongs of the Magela Creek, can be used for accurate age determinations.

#### 6.4 Growth

##### 6.4.1 Growth description

Asymptotic growth equations have been widely used to describe growth in animals, as they fit the empirical data adequately enough, and because their constants have been interpreted as having at least some biological meaning. Using the growth of freshwater mussels as an illustration, Haukioja and Hakala (1979) made a thorough appraisal of asymptotic growth equations. They concluded that none of the parameters of the equations had any significant biological validity, when comparisons of parameters derived from different populations were made. The best known and most commonly used growth equation in fisheries assessments, is the von Bertalanffy equation (von Bertalanffy, 1957). It has come under criticism over the reality of

asymptotic growth (Knight, 1968) and with specific reference to marine bivalves, has been shown to provide an inadequate description of the growth of the early stages (Theisen, 1973; Yamaguchi, 1975). Nevertheless, when applied to appropriate data, the von Bertalanffy equation is generally considered a good approximation of observed growth curves. In relation to growth of marine bivalves for example, Brousseau (1979) found the equation a valuable model when comparisons of growth patterns in single-species populations were made, providing large numbers of animals were used and the entire size range of animals was considered, especially the older age classes.

Although widely applied to growth of marine bivalves, it is only in recent times that the von Bertalanffy equation has been used to describe growth of freshwater mussel populations (Kenmuir, 1980; Walker, 1981b; Dudgeon and Morton, 1983; McCuaig and Green, 1983). Coon et al. (1977) used general power functions to describe growth of freshwater mussels in pools of the Mississippi River. For some North American populations of Anodonta grandis growth does not tend to a maximum length and therefore growth according to the von Bertalanffy equation is invalid (Green, 1980). For these populations, Green (1980) developed a growth model that did not assume an asymptotic size.

As applied to linear growth, the von Bertalanffy growth equation is:

$$l_t = L_\infty [1 - e^{-K(t-t_0)}]$$

where  $l_t$  = length at any given time  $t$ ,

$L_\infty$  = the theoretical average maximum length,

$K$  = the growth constant indicating the rate at which length approaches  $L_{\infty}$  ,  
 $t_0$  = the calculated time at which length is equal to zero.

Conventionally, the suitability of the von Bertalanffy growth model for growth rate data has been tested using Walford plots of lengths at consecutive ages. With asymptotic growth and a constant decrease of growth rate with age, the mean age values should give a linear relationship on a Walford-graph where the slope of the line is equal to  $e^{-K}$ , and the intersection of the line and the 45° diagonal from the origin, is at the asymptotic value of length,  $L_{\infty}$  (Walford, 1946). Variations of the Walford plot may be used to test the suitability of other growth models for growth rate data. Kaufmann (1981) presented techniques involving such variations of the Walford plot, for determining which of several growth curves - exponential, power, Gompertz, logistic, as well as the von Bertalanffy - could best fit growth data. Other than the von Bertalanffy model, the appropriateness of a particular growth curve is indicated by the linearity of the relationship between specific growth rate and size, after the axes have been suitably transformed.

Using Kaufmann's (1981) methods with growth rate data of V. angasi, untransformed plots of specific growth rate and size consistently gave the best linear fit of data from among all the Magela Creek populations. This indicated that the von Bertalanffy model was the most suitable of the models tested. Walford plots are shown in Figure 6.10 for mean length for age data from representative mussel



populations in Georgetown, Mudginberri and Nankeen billabongs. From Figure 6.10, and exemplifying the results of the Kaufmann technique just described, it is clear that for most billabongs and age classes, linear relationships of lengths at consecutive ages are found, indicating that the von Bertalanffy model sufficed for the growth data.

As observed from the plots (Fig. 6.10), however, and from others drawn for populations in other waterbodies (not shown), growth of young-of-year mussels does not conform to the growth equation. Because of this unconformity, the Walford plots of growth data of V. angasi resembled to some extent those of the arctic population of A. grandis studied by Green (1980); Green found that a quadratic model more adequately described the relationships in the Walford plots. With the assumption of nonlinearity, he derived a model for the population that did not assume an asymptotic size. For all populations of V. angasi, however, inclusion of a quadratic term in the Walford plot relationships added no extra significance over the linear model. This indicated asymptotic growth of the populations (and therefore growth according to the von Bertalanffy model).

Thus, the cause of nonlinearity in the Walford plots was the inclusion of growth data of young-of-year mussels only. As recommended by Ricker (1975), therefore, this age class was rejected whenever the von Bertalanffy curve was fitted to the growth data. The value for K (the slope of the Walford line) of the Georgetown mussel population changes with age with two growth stanzas either side of a length of about 55 mm. This is a common enough phenomenon in fish populations (Ricker,

1975), and also in some marine bivalve populations where Johannsen (1973) for example, represented growth of Venerupis pullastra with two von Bertalanffy equations about a critical size. Different growth stanzas were sufficiently uncommon (see Corndorl, Fig. 6.11 and section 6.4.3.2) in populations from other billabongs to warrant that only one equation be used to describe growth of each billabong population. Although this probably led to some loss of precision in the values of the growth constants, a single equation was nevertheless a more useful aid for comparisons between the growth of populations in all waterbodies.

Computations of the von Bertalanffy growth parameters were performed using the interative method developed by Allen (1966). Whilst this method is regarded as amongst the most precise (Ricker, 1975), additional advantages are: the allowance for data collected at any age interval; the parameters of the equation may be calculated using individual observations (thus making use of all the available data); and estimates of the limits of error (confidence limits) of the parameters are provided. Individual lengths and ages of mussels at the time of collection were used in the computations. To set specific ages, it was necessary to have suitable arbitrary reference points of the times of larval metamorphosis and annulus formation. Annulus formation is seen with early Wet season flushing of the creek (section 6.3.3.2), and 1 January served as a suitable and convenient reference date for this. The times of juvenile settlement were extrapolated from mean lengths for age data of juveniles collected about the time of recruitment as depicted in Figures 6.2-6.4 and elsewhere (not shown). These dates are: Georgetown - 7 March; Mudginberri, Buffalo,

Island - 10 January; Nankeen - 11 March. For other waterbodies these data are not available, but for the general knowledge that recruitment occurred during the Wet. A mid-Wet season date of 1 February therefore was arbitrarily set for the time of recruitment in these places.

#### 6.4.2 Growth within and between waterbodies

##### Within billabongs

Growth data were available between sampling stations in Georgetown, Mudginberri and Buffalo billabongs, and between different depths in the floodplain billabongs, Leichhardt and Nankeen. Sampling stations within the billabongs are the ones used for routine monthly collections, as described in section 3.1. Tables 6.3-6.7 show the parameters of the von Bertalanffy growth equation and their 95 per cent confidence intervals (calculated by Allen's (1966) method) for mussels within different localities of the billabongs. The equations were calculated at each site, for each sex separately, and overlap in the confidence intervals for a particular parameter, indicated that no significant differences were observed between the sexes. In practice, sexual differences were rarely found and the parameters calculated for the sexes combined only are shown. In Georgetown billabong, however, marked sexual differences in growth patterns were observed within sites, and Table 6.3 shows the parameters calculated separately and combined for the sexes. Clearly from Tables 6.3-6.7, growth rates may differ considerably between mussels at different sites of the same billabong (and occasionally between the sexes at the same site), and

apparent trends and their significance are discussed in section 6.4.3.1.

#### Between waterbodies

The variation in growth between waterbodies was more marked than within billabongs. For between-waterbody comparisons therefore, growth data were combined for each waterbody. Tables 6.8-6.19 show the means, standard deviations, 95% confidence intervals and ranges of lengths for each age class of mussel in the different waterbodies, calculated separately and combined for the sexes. From these data the enormous variation in size range within a particular age class is most apparent, and shows that mussel size from small samples may bear little resemblance to age. Further, this factor is offset only to a minor degree when within-billabong variation is considered. (Data not shown.) von Bertalanffy growth parameters were calculated separately and combined for the sexes from these data (Table 6.20). Again, from the confidence limits of both data sets, growth differences between the sexes are trivial, and all further comparisons were based upon the growth parameters calculated for the sexes combined (Table 6.20). von Bertalanffy growth curves calculated for the combined sexes, are shown with means and confidence limits of size at each age interval, for the different waterbodies in Figures 6.11 and 6.12. Marked differences are noted in the growth rates of mussels between different waterbodies. Apparent trends and causes of the disparities are discussed in section 6.4.3.2.

#### 6.4.3 Environmental determinants of growth

Of the three parameters of the von Bertalanffy equation,  $L_{\infty}$ ,  $K$  and  $t_0$ ,  $L_{\infty}$  and  $K$  are interpreted as having intrinsic physiological significance, by which growth within populations may be studied or compared between populations. Haukioja and Hakala (1979) concluded that asymptotic growth parameters in general, were unsuitable for comparing growth between populations of Anodonta piscinalis. However, they found the von Bertalanffy equation least unsuitable for producing parameters for comparisons between populations and did not rule out the possibility that the parameters in general may be correlated with some environmental factors or other parameters of growth. Haukioja and Hakala recommended length at a critical annulus for comparing growth rates between populations but stated that this criterion would not be valid if the groups compared had clearly different final lengths. McCuaig and Green (1983), however, used analysis of covariance of linear Walford regression equations to test hypotheses about perturbations that might bring about differences. With such analysis, they found the parameters apparently quite sensitive to hypothetical perturbations, with subsequent changes to population growth.

The constants,  $L_{\infty}$  and  $K$ , derived from growth equations of mussel populations in the Magela Creek, were fairly easily interpreted, together clearly dictating the form of growth within and between the populations in most waterbodies. With the aid of hypothetical growth curves, they were of considerable use for investigating some important factors that might determine growth patterns of mussels. These

factors are discussed below.

Reiterating, as an aid to the following discussion, the constant  $L_{\infty}$  is the theoretical asymptotic size of an organism while  $K$  describes the rate at which this value is approached. Both Ralph and Maxwell (1977) and Brousseau (1979) considered the constant  $K$  of interest, because it could be used to make comparisons of the rate of growth of different (bivalve) species or of the same species from different environments. Use of the parameter in isolation in this manner, however, must be viewed with caution for as Ricker (1975) states,  $K$  is a growth coefficient, not a growth rate. A relatively large  $K$  value for example, merely suggests that the asymptotic size is approached relatively early in life, while a lower  $K$  value may yet describe a population whose growth rate at all ages is higher. Thus growth rates in between-population comparisons can only be studied with knowledge of both  $K$  and  $L_{\infty}$ . Ricker (1975) states that for any given initial size of an organism, a larger  $K$  means a smaller  $L_{\infty}$  and thus slower growth from that time onward. Ricker's mathematical basis and argument for this statement (p.221) is apparently incorrect (V. Bofinger and W. Taylor, pers. comm.) on the basis of assuming the variable  $l_t$  to be a fixed and constant value. Nevertheless, the statement is probably true for most populations, including at least marine bivalves (Theisen, 1973).

With respect to the interpretation of and interrelationships between the growth constants of the von Bertalanffy equations derived for mussel populations within and between waterbodies of the Magela Creek, three types of comparative growth relations were found. The

hypothetical types are shown in Figure 6.13. In type A relations, both populations reach the same maximum size ( $L_{\infty}$ ), but at a slower rate for those on the bottom curve, characterised by a lower  $K$ . In type B relations, a smaller  $K$  means a larger  $L_{\infty}$  (and vice versa). Over the whole lifespan nevertheless, lower  $K$  populations are faster growing than populations with successively higher  $K$  values. A smaller  $K$  may also mean a larger  $L_{\infty}$ , but for type C relations, higher  $K$  populations may reflect faster growth rates relatively earlier in life before being surpassed in growth rate by lower  $K$  growth for the remainder of the lifespan.

Beverton and Holt (1957) noted that  $K$  could be regarded as independent of the level of feeding but might be expected to vary with certain environmental factors such as temperature. (These comments were directed to temperate fish species.) These authors provided evidence that the parameter  $W_{\infty}$  (asymptotic weight,  $W_{\infty} \propto L_{\infty}^3$ ) was affected by variations in food consumption. Even if changes in  $K$  occurred for various levels of food consumption, Beverton and Holt suggested that  $K$  may be expressed in terms of  $W_{\infty}$  and from the theoretical point of view then only  $W_{\infty}$  need be used in attempting to predict the growth rate in given circumstances. In the Magela Creek populations, type B relations were typical of between- and most within-billabong comparisons of growth (see below). Thus  $L_{\infty}$ , in a loose sense, in type B comparisons is more indicative of growth rate throughout all life-stages (by nature of the shape of the curves) than the false impression that  $K$  values on their own would suggest. In any case,  $L_{\infty}$  and  $K$  were mostly negatively correlated in type B relations (section 6.4.3.2). As only food availability was of interest as a quantitative

determinant of growth rates, and as  $L_{\infty}$  may (1) on theoretical grounds be dependent upon the feeding level, (2) be indicative of overall growth rate and (3) nevertheless be correlated with  $K$  in type B comparisons, the parameter  $L_{\infty}$  only was considered for study. A further reason for the choice of  $L_{\infty}$  as a measure of growth rates, is that it was a more conservative parameter, not influenced to the same degree as  $K$ , to weighting of the age classes and varying age structures.

Regression analyses were performed where each parameter,  $L_{\infty}$  and  $K$ , was regressed against itself where the parameter was derived from computations using individual observations, as opposed to unweighted mean observations for each age class. The analyses showed highly significant correlations in both cases ( $P < 0.001$ ), but  $K$  calculated with unweighted means accounted for only 77% of the variation in  $K$  calculated from individual observations, as opposed to a high 95% of the variation in  $L_{\infty}$  derived from individual observations that was accounted for by  $L_{\infty}$  derived from unweighted means. Thus, differences in sample sizes and age structures between billabong populations that were used to compute the growth equations, affect  $K$  more than  $L_{\infty}$ . The constant  $K$  in relation to growth is apparently more complex in its interpretation than  $L_{\infty}$ . Further discussion on its significance is made in the following sections.

#### 6.4.3.1 Within billabongs

The mussels on the shallower and sandier transect of Georgetown billabong represented the only population in the Magela Creek where



sexual differences in growth rates were observed (Transect B, Table 6.3). Over the entire size range, females grew at a significantly faster rate than males (i.e. a type B relation, Fig. 6.13). Mussels in this region of the billabong regularly move onto the adjacent flooded peripheral shores during the Wet (section 6.8.1). Growth on the flooded shores during this time occurs at a faster rate than of mussels in deeper waters (unpublished observations and data). Some differential movement of females onto the peripheral shores was observed at these times (section 6.5.1), but whether these differences are enough to explain why females might overall grow more quickly than males, however, is not certain. With growth data combined, growth between mussels on the two routine transects of Georgetown billabongs is one of type A as illustrated in Figure 6.13. Both populations reach the same asymptotic size, but the population on the shallow, sandy transect does so at a faster rate than the population on the deeper, muddy transect. The preponderance of younger mussels on the shallower transect (mean age of 4.20 years as opposed to 6.54 years on the deeper transect) may have considerable influence on the values of the parameters of the growth equation here. Young mussels predominate in the billabong generally (Fig. 6.29) and the values of  $K$  and  $L_{\infty}$  derived from individual observations of the mussel population in the billabong as a whole, are 0.290 and 62.8 mm respectively, as opposed to corresponding values of 0.164 and 67.4 mm when the parameters were calculated from unweighted data of mean lengths for each size class. In the former, calculations were biased towards the younger age classes, but the unweighted data favoured the older age classes. Thus the type A relation between the two transects can be best explained at this stage by the difference in age structures of the two populations.

Tables 6.4 and 6.5 show the von Bertalanffy growth parameters calculated for data between the routine sampling stations in Mudginberri and Buffalo billabongs respectively. Growth within each billabong varies considerably. The growth relations when plotted were of Type B (Fig. 6.13), and only a few populations in Buffalo billabong contradicted this pattern. Thus asymptotic size indicated growth rates of populations within the billabongs, and was used as the dependent variable denoting growth quality of mussels in subsequent correlations of environmental determinants of growth.

As  $L_{\infty}$  may theoretically be expected to vary with food availability, chlorophyll levels as a measure of this, were compiled for different regions of the two channel billabongs. For Buffalo billabong, crude estimates of chlorophyll content of the waters were available only. The waters of the 10 sites sampled in the billabong were analysed on two occasions during 1981 for chlorophyll. The levels and mean values are shown in Table 6.22. Within-billabong variation of chlorophyll in Mudginberri, was reported in Kessell and Tyler (1983). Chlorophyll concentrations were calculated fluorometrically on four occasions during 1980 and 1981, over different regions of the billabong. The data in Kessell and Tyler (1983) for each sampling occasion, are divided into 5 equal ranges of chlorophyll concentration, classed from lower to higher concentration as 1-5, and mapped over the respective billabong regions. The concentrations on these occasions (in arbitrary units) and mean values, over the routine sampling stations for mussels are shown in Table 6.21. From the limited data, there is a trend in both billabongs for chlorophyll concentrations (and

presumably primary productivity), to be higher at the southern end of the billabongs, and over the more organic sediments (stations 6 and 7 in Buffalo, and 3 and 4 in Mudginberri Fig. 3.1). Chlorophyll concentrations were regressed against asymptotic size of mussels between the different sites of both billabongs. For Mudginberri billabong, a very significant ( $P < 0.01$ ) logarithmic correlation was found (Fig. 6.14), whilst for Buffalo, a significant ( $P < 0.05$ ) linear correlation was found between asymptotic size and chlorophyll concentration (Fig. 6.15). Both results provide good evidence that food availability as measured by algal concentrations, is a chief determinant of mussel growth rates within billabongs. Whilst mussel growth rates are generally highest over the organic sediments, of further interest is the observation that on some of these sediments (station 3 in Mudginberri, and station 2 in Buffalo) mussels grow faster than the surface chlorophyll values would suggest. This may be an artifact of the small sample numbers that comprise the mean chlorophyll values, but may suggest that in addition to the nutrients made available for algal production, breakdown and resuspension of the organic material in the sediments conceivably provides an additional, and unmeasured detrital food supply for mussels here.

Plots of the growth curves for mussels from different depths of Leichhardt and Nankeen billabongs (Tables 6.6 and 6.7 respectively), showed Type B relations for Leichhardt and Type C relations for Nankeen billabong (Fig. 6.13). Thus growth rates in Leichhardt billabong decrease with depth. A similar pattern is observed in Nankeen for about the first 13 years of life, before overlap of the curves (Fig. 6.13) reverses the growth rate order, and growth rates

actually increase with depth. Declines in food supply and temperature with depth have elsewhere been used to explain decreases in mussel growth rates with depth (see Appendix 3).

Some limited chlorophyll data are available between the surface and bottom waters of both billabongs as a check of differences in food availability with depth that may correlate with growth rates. Over a 10 month period (Fig. 2.29), surface chlorophyll concentrations in Leichhardt billabong averaged 15.5 as opposed to 13.3  $\mu\text{g}/\text{l}$  in the bottom waters. Over 9 months of readings in Nankeen billabong, surface chlorophylls averaged 7.0 as opposed to 9.1  $\mu\text{g}/\text{l}$  for bottom water concentrations. Thus, decreasing food availability might explain the growth rate decline of mussels with depth, in Leichhardt billabong, and vice versa for the greater maximum lengths attained at depth in Nankeen. In Leichhardt billabong, decreasing oxygen tensions with depth (notably severe in this billabong, section 2.3.2.2) very likely reduce the time available for feeding, further adding to the growth rate reduction of mussels with depth here. While decreasing oxygen concentrations with depth in Nankeen might similarly explain the slower growth rates of mussels at depth at least for the relatively younger age classes, some other overriding factor reverses this pattern later in life. Apart from perhaps increasing food availability with depth that might support better growth in the later years, shallow water stunting later in life might also explain the pattern. Nankeen billabong is possibly the most exposed billabong on the Magela Creek, and becomes extremely turbid during the latter period of the Dry season (section 2.3.2.4). Wave-induced resuspension of the silty sediments no doubt, is quite severe in the shallow waters

of the billabong at this time. The wave action and/or the high amounts of suspended solids that may interfere with feeding, may reduce growth rates of mussels in the shallow waters (section 6.1). If this is the case, then the factor(s) are apparently selectively inhibitive to the growth of the later year stages.

#### 6.4.3.2 Between waterbodies

Growth curves calculated for populations of mussels from each waterbody (Figs 6.11 and 6.12) when compared with one another are of Type B relations (Fig. 6.13). Thus as  $K$  increases,  $L_{\infty}$  becomes smaller (and vice versa), and  $L_{\infty}$  is indicative of growth rate over all age classes. A significant ( $P < 0.05$ ) negative, linear correlation was found between the estimates of  $L_{\infty}$  and  $K$  calculated with data from each waterbody (Fig. 6.16). (Not enough growth data were available for Gulungul and Hidden billabongs for the estimates of their growth parameters to be considered reliable. The data from these billabongs are hence omitted from Fig. 6.16 and from further calculations and discussions.)

From Figures 6.11, 6.12 and 6.16 some general statements may be made. A low  $K$  constant is indicative of a population whose growth is continuous throughout the whole lifespan, whereas a high  $K$  indicates maximum size is attained relatively earlier in life. The former populations occur in billabongs where food availability is high (shown later) for much of the year and which is capitalised upon by even the older age groups (Island, JaJa, Leichhardt and Jabiluka). In other waterbodies, the food supply may be low (Georgetown, Magela Creek

channel, Buffalo), or relatively more abundant (Nankeen), but nevertheless is available for only a short period of the year. Growth in these waterbodies is apparently accomplished earlier in life and the older age groups do not grow much on a low food supply, nor capitalise upon a more abundant but short-lived supply.

From Figure 6.16, Corndorl and Mudginberri populations (points 9 and 12 respectively) have apparently anomalous K values, being lower than might be expected in relation to the values of the parameter in other waterbodies. The Mudginberri population shows a steady increase in size over the whole life span (Fig. 6.11). The food supply in this billabong on average is low, but is probably more evenly spread out over the year (Fig. 2.28). This factor, in addition to the general equitableness of the billabong waters by comparison to the other waterbodies (e.g. low turbidity, high oxygen content), may be more conducive to growth throughout the lifespan of individuals in the population. In Corndorl, growth of the mussel population is in two stanzas either side of an age of 12 years (Fig. 6.11). The older year classes appear to be growing at a different and faster rate than the younger ages. This might be attributed to either some major and abrupt shift downwards in food abundance over the years, or selection may favour faster growing individuals at some stage in life. The latter suggestion is conceivable in unstable and shallow, backflow environments where, if the waterbody occasionally dried up, only the larger individuals of the early year classes may survive by virtue of their higher tolerances to desiccation (unpublished data). Thus, the growth pattern of the Corndorl population is an anomaly and the presence of two growth phases results in a relatively low K constant

when the growth equation is derived from the pooled population data.

As asymptotic size,  $L_{\infty}$ , may be regarded as dependent upon the level of feeding, a relationship was sought between  $L_{\infty}$  estimated for each waterbody population and algal production as measured by mean seasonal chlorophyll concentrations (Table 2.7). Figure 6.17 shows the relationship. Neither a Gompertz nor logistic curve adequately fitted the data, and a line of best fit was drawn by eye. The comparatively low  $L_{\infty}$  estimated for the mussel population in Leichhardt billabong (No. 24), is no doubt due to a preponderance of young mussels in the billabong and a corresponding lack of size classes of greater age (Figs 6.12 and 6.30). Each has the effect of lowering the asymptotic size in a weighted calculation. Nevertheless and clearly, growth rates can be predicted quite accurately and simply with knowledge of mean chlorophyll concentrations. With the regression equation of the constant  $K$  in terms of  $L_{\infty}$  (Fig. 6.16), the growth dynamics of individual mussel populations can be even better understood.

## 6.5 Population structure

### 6.5.1 Distribution of the sexes in billabongs

Sex was determined for large numbers of mussels between the routine sampling stations (Georgetown, Mudginberri and Buffalo) and/or different depth regions of billabongs (Georgetown and the floodplain billabongs). Chi-squared tests were performed to determine whether or not the sexes were distributed evenly across the different habitat types sampled within each billabong. Data from floodplain billabongs

were tested alone, and lumped together in a single test across all billabongs. No trends in sex ratios within billabongs were evident, and the chi-squared tests revealed no significant deviations in any case of the proportions of the sexes between sites or different depths of billabongs that would suggest that the sexes were unevenly distributed.

An additional test was performed in Georgetown, for data of sex distribution of mussels across the shallow, sandy transect that incorporated shallow inundated banks during the Wet season. Adult mussels make seasonal movements up onto, and back away from the inundated shore (section 6.8.1). 36 out of 69 adult mussels (52%) collected from the inundated shore were female as opposed to 429 out of 895 adults (48%) along the entire transect. However, a chi-squared test, revealed that there was no differential movement of females onto the flooded shore ( $\chi^2 = 0.55, P > 0.25$ ).

## 6.5.2 Size distribution

### 6.5.2.1 Within-billabong patterns

Length was measured of all mussels that were sampled for density estimates in the different habitats of the billabongs. The sampling rationale and methods are described in section 5.2. While density estimates for Georgetown billabong were derived from late Dry season sampling, size data, however, were obtained from the routine monthly collections made over the entire duration of the study. Mean lengths per substrate and depth interval within the Magela Creek billabongs



are shown in Tables 6.23 - 6.28. Two-way analysis of variance was performed on the habitat means wherever applicable to determine whether there were significant differences in mean lengths among depths or in mean lengths among different substrates.

### Depth

No significant differences were found in size among depths in Georgetown, nor in size between locations ( $P > 0.05$ ) when data were analysed according to depths and the two routine transects sampled in the billabong. However, partitioning of the sum of squares (SS) due to depths into linear, quadratic and residual components revealed a very significant ( $P < 0.01$ ) linear effect. With the data of both transects pooled, however, further regression analysis showed a very significant ( $P < 0.01$ ) quadratic relationship. The regression equation is described in Table 6.29, and the relationship plotted in Fig. 6.18. Thus mussel size increases with depth in Georgetown, reflecting the observations that recruitment occurs in the shallow reaches of the billabong, and young mussels move into deeper waters with age (sections 6.6.1 and 6.8.1). A slight decrease in size was recorded in the deepest reaches of the billabong (Fig. 6.18). This can be attributed to slower growth rates of mussels here rather than the presence of younger age classes, because mean age increases with depth in the billabong (Fig. 6.25). This might be due to oxygen deficiencies at depth, or more likely to the high amounts of suspended solids that occur during the Dry season and which are generally inhibitive to algal production at these depths (and hence food availability) (Fig. 2.28). Suspended solids might also interfere with

the normal feeding processes if the load is greater with increasing depth in the billabong.

In Gulungul billabong, mussel size tends to increase with depth (Table 6.24), though not enough depth intervals were sampled for a significant regression to be fitted to the data. It would appear almost certain that the older age classes would dominate at depth, as the billabong occasionally dries out, and mussels in deeper waters would be more likely to survive these periods. Analysis of variance showed no significant differences in size among depths in Corndorl when data were analysed according to the two major substrate types of the billabong. Partitioning of the depths SS, however, revealed a significant ( $P < 0.05$ ) linear effect. As no substrate effects were found, the data were pooled. The resulting linear regression equation is described in Table 6.29, and the relationship plotted in Figure 6.19. Unlike Georgetown and Gulungul, mussel size in Corndorl billabong decreases with increasing depth. Again, either decreasing mean ages or growth rates with depth can account for this observation. Unfortunately no age data are available in relation to different depths of this billabong. Nevertheless, both decreasing oxygen tensions and consolidation of the sediments with increasing depth were observed in Corndorl. Both factors have the potential to reduce growth rates of mussels and even induce early mortality, thus shortening the lifespan of mussels at depth. Low oxygen concentrations may effectively shorten the period available for feeding, thereby affecting the growth rates of mussels, or effectively alter the age structure to favour younger mussels by killing off older mussels. The siltier environment associated with the very soft

sediments of the deepest waters may also interfere with feeding, and with age, more energy may be required to maintain a hold in the soft sediments to the detriment of energy allotted to growth. When the sediments are extremely soft, mussels may reach a threshold size which the sediments are unable to support and mussels may consequently smother and die prematurely. This factor, however, cannot explain why mussel size decreases with depth over the relatively more consolidated sediments along the northern bank of the billabong (Table 6.25). The sediments, are notably siltier with increasing depth. From the limited information, food availability may not be a factor in reducing growth rates with depth, as chlorophyll concentrations tend to be greater at depth in Corndorl (Fig. 2.28). Shoreward migration with age to avoid the deepwater stresses mentioned above could explain the observed size distribution.

No significant differences were found in mussel size among the different substrate types in either Mudginberri or Buffalo billabong. Data among substrates were pooled for each billabong, and a single analysis of variance was again used to test for differences in mussel sizes (1) between billabongs, and (2) among different depths. No differences were found in sizes between billabongs, but significant differences occurred in size among depths ( $P < 0.05$ ). While partitioning of the depths SS revealed a very significant linear effect ( $P < 0.01$ ) with the data of both billabongs pooled, further regression analysis showed an even more significant ( $P < 0.001$ ) logarithmic relationship between mussel size and depth. The regression equation is shown in Table 6.29 and plotted in Figure 6.20. The increase in mean size of mussels with depth in the channel

billabongs is caused by, at least, an increase in mean age over the same gradient (Fig. 6.26). To some extent, primary productivity is also high over the deepest portions of these billabongs (Tables 6.21 and 6.22), and so the larger sizes of mussels are partly related to the higher growth rates here.

Mean length among the 10 sampling stations in Nankeen billabong did not differ significantly. Nor were significant differences found in size among different depths when averaged over the sites. An analysis of variance was performed with size in relation to billabongs and depth, over the five floodplain billabongs. No significant differences were found in mussel size among billabongs, nor in size among depths. However, partitioning of the depths SS showed a significant quadratic effect ( $P < 0.05$ ). The relationship is described in Table 6.29 and plotted in Figure 6.21. An intermediate depth is found at which size reaches a maximum in the floodplain billabongs. Again, the relationship is mirrored by the same pattern in the age distribution of mussels in these billabongs, where a maximum age occurs at the same intermediate depth (Fig. 6.27).

In general, size variation of mussels in relation to depth in the Magela Creek billabongs, can be explained by the same variations in mean age. No age related data were available for Gulungul and Corndorl billabongs, but if size in these billabongs is a reflection of the age distribution (as in the other billabongs) then mean age increases with depth in Gulungul but decreases with depth in Corndorl. If this is the case, then substrate- and/or oxygen-related factors might best explain why older mussels avoid or succumb in the deeper

reaches of Corndorl billabong.

### Substrate

As seasonal movements of at least a portion of the Georgetown population are likely to bring mussels into contact with a variety of the sediment types of this billabong (section 6.8.1), no analysis of size distribution in relation to substrate was undertaken here. Nor did the relatively homogeneous sediments of Gulungul and the floodplain billabongs provide opportunities for such study. As mentioned earlier, no significant differences were found in mussel sizes between the two substrate types in Corndorl billabong.

No significant differences were found in mean size of mussels among different substrates in either Mudginberri or Buffalo billabongs. Using mean sizes per substrate type over all depths sampled, differences in sizes were tested for among comparable substrates in both billabongs. No significant differences were found in mussel sizes between the two billabongs, but significant differences were found in sizes among the different substrates ( $P < 0.05$ ). As for the analysis performed in section 5.4.1.2.1, the four sediments were ranked in order of increasing organic content and decreasing particle size. The substrates SS was then partitioned into linear and residual components. This revealed a very significant linear effect ( $P < 0.01$ ) with mean sizes increasing over the gradient from sand, to the relatively siltier and increasingly unconsolidated and organic sediments (Fig. 6.22). While the more organic sediments generally harbour relatively older mussels in the channel billabongs (section

6.5.3.1), the increase in mean size over the gradient of increasingly organic sediments can also be attributed to the same trend in faster growth rates of mussels as previously found (section 6.4.3.1).

#### 6.5.2.2 Between waterbodies

For size distribution analysis between all waterbodies, quantitative data from all routine monthly collections were used. This meant that only in the billabongs - Georgetown, Mudginberri, Buffalo and Nankeen - did non-selective sampling ensure that all the size classes were represented (section 3.2.1). Nevertheless, for size classes above about 20 mm (section 3.2.2), the data between waterbodies are assumed comparative. Table 6.30 shows the mean lengths, their standard deviations, maximum and minimum lengths and sample sizes of mussels recorded from all waterbodies. Figures 6.23 and 6.24 show the length frequency distributions of mussels from the various waterbodies. From these figures an ubiquitous adult mode is apparent. This large and often single mode reflects similar, unimodal age distributions (Figs 6.29 and 6.30), where overlap in size of the adult age classes is considerable, and where young mussels may be sparse or approach adult size very rapidly. The trough between the juvenile and adult mode of the Mudginberri, Buffalo and Nankeen mussel populations, represents high seasonal recruitment followed by significant juvenile mortality before the young approach adult size. Only in Georgetown billabong do the size distributions represent regular year-to-year recruitment where numbers of mussels gradually decrease with increasing age (Fig. 6.29). The bimodality of Gulungul size distributions is a direct reflection of a trough of missing age classes in the age structure of mussels in the population (section 6.7.3).

The mean sizes of mussels in the different waterbodies (Table 6.30) is clearly related to differences in growth rates, even though the mean length is overestimated to some (slight) degree in populations where very small mussels were not collected or were uncommon. Like asymptotic size ( $L_{\infty}$ ) therefore, mean length correlates with mean chlorophyll concentration of the waters, the latter reflecting a measure of food availability. No statistical treatment of these data, however, was undertaken.

### 6.5.3 Age structure

The age data derived from mussels collected at routine monthly intervals in the waterbodies, were used for the following age structure analysis.

#### 6.5.3.1 Within billabongs

Sufficient quantitative data were available for Georgetown, Mudginberri, Buffalo, Leichhardt and Nankeen billabongs, for within-billabong study. Because of the seasonal movements of mussels over the sediments in Georgetown, the limited number of sampling stations within Mudginberri and Buffalo, and the relatively homogeneous bottom types of Leichhardt and Nankeen billabongs, analyses were restricted to relationships between age and depth only. Mean ages per depth interval within the billabongs are shown in Tables 6.31 - 6.34. Again, two-way analysis of variance was used as the test basis for studying these relationships.

No significant differences were found in mean age among depths in Georgetown, but a significant difference in mean age of mussels ( $P < 0.05$ ) was found between the two routine transects sampled in the billabong. Mussels on the sandy, shallow transect were significantly younger than those further downstream on the muddy and relatively deeper transect. While partitioning of the depths SS would most likely have yielded a significant linear effect, plots of mean ages and depths for each transect suggested logistic relationships would be more appropriate models. The fitted functions are described in Table 6.35 and are plotted for each transect in Figure 6.25. As for the same pattern in size distributions within the billabong, the increase in age with depth along each transect can be interpreted by peripheral recruitment, with young mussels moving into deeper waters with age. Presumably, this response is a gradual one and is a reaction to falling water levels and increasing water temperatures that accompany the progress of each Dry season. By the end of particularly dry years especially, mussels would be left in the little remaining waters, of the deepest portions of backflow billabongs. The observation is probably modified to some degree by the increased mortality that might be expected in the shallows from desiccation, high water temperatures and mammalian predation.

For the same depth intervals in Georgetown billabong, mussels are younger on the shallow, sandy transect than further downstream on the deeper, muddy transect. Recruitment on the shallower transect is disproportionately high. 385 out of 2436 mussels collected on this transect were less than a year old compared to only 493 out of 2658



further downstream. The large numbers of juveniles on the shallower transect therefore have a significant influence on the mean age structure here. The shallower transect is also presumably, a less stable environment than further downstream. In particularly dry years, high mortality may result from high water temperatures, desiccation and predation. This region of the billabong is also susceptible to scouring during Wet season floods, and the population on the sandy sediments may be periodically removed during such events (section 5.4.1.2.1). It is tempting to suggest that the significant recruitment observed over this transect is some form of density dependent compensation for the relatively fewer adults that occur here. Conditions here, however, may be particularly well suited to the needs of juveniles as opposed to elsewhere (section 6.6.1).

Significant ( $P < 0.05$ ) and highly significant ( $P < 0.001$ ) linear regression relationships were found between mean age and depth in Mudginberri and Buffalo billabongs respectively. The regression equations are described in Table 6.36 and plotted in Figure 6.26. Mean age increases with increasing depth in both billabongs. Unlike Georgetown, there was little evidence to show that recruitment was higher in the shallower waters or that mussels moved to deeper waters with age (section 6.6.1). To some degree, the deeper reaches of the billabongs are out of the mainstream flow, where silt and detritus are able to settle. Thus older mussels occur on these sediments in Mudginberri (sites 3 and 4 in Table 6.32) and to some extent in Buffalo billabong (sites 2, 6 and 7 in Table 6.33). Some sandy sites in both billabongs are presumably relatively unstable and shifting, and younger mussels may be expected there because of this. Sites 1

and 2 in Mudginberri (Table 6.32) and sites 8, 9 and 10 in Buffalo (Table 6.33) are examples of these. Site 8 in Buffalo occurs in a narrow neck of the billabong (Fig. 3.1), where stream velocities were observed to be particularly high during the Wet. The shifting sands here bear few mussels but those that are present are relatively young. The mussels in fact, were so young for the observed depth that the site was omitted from calculation of the linear regression equation (Fig. 6.26). Nevertheless, other sandy sites in Buffalo billabong harbour relatively older mussels (sites 1 and 4) and are therefore presumably quite stable. The clean waters of both billabongs can expect relatively high bottom water temperatures particularly over the late Dry (Table 2.6). The warmer environment in the shallower reaches may be stressful and thereby stimulate mussels to move to deeper waters. The higher temperatures may also increase metabolic rates enough to induce an earlier mortality of mussels in the shallows much as suggested for other bivalves (Appendix 3). High growth rates were found for mussels in some shallow reaches of Buffalo billabong (Fig. 6.15).

Highly significant differences were found in mean age among billabongs, and in mean age among depths ( $P < 0.001$ ) when data were analysed according to the five floodplain billabongs. Partitioning of the depths SS showed highly significant ( $P < 0.001$ ) quadratic effects. Significant quadratic relationships between age and depth were found for Leichhardt ( $P < 0.01$ ) and Nankeen ( $P < 0.001$ ) billabong. The regression equations are described in Table 6.36 and plotted in Figure 6.27. An intermediate depth is found in the floodplain billabongs at which age reaches a maximum but about which mean age of mussels

decreases. In the floodplain billabongs, recruitment occurs in the littoral zones (section 6.6.1), and either progressive movement to deeper waters with age, increased mortality in the shallows, or both, may explain the progressive increase in age of mussels with depth. Movements are presumably associated with avoidance of the resuspended silty sediments that are likely to be accentuated in the shallows, avoidance of high water temperatures, desiccation and predation. Mussels might also suffer significant mortality from these factors and even the higher growth rates of mussels in at least the early life stages in the shallows, by some physiological mechanism, might shorten the life span. Mussels reach a maximum age at an intermediate depth beyond which they become progressively younger. Older mussels could conceivably migrate shoreward with increasing age to avoid the hazards associated with the greater depths. Significant mortality of older mussels at greater depths is also likely. Dissolved oxygen depletions that may be severe at depth in the floodplain billabongs are almost certainly the major stresses that induce both movement of older mussels away from, and premature mortality of the older age classes in, the deepest reaches of the billabongs.

In all of the billabongs studied, mean age increases with increasing depth. Both increased mortality in the shallows, and avoidance with increasing age of these regions with all their hazards can account for this observation. Only in floodplain billabongs, were mean ages observed to decrease at the greater depths, again adding strong support to the view (section 5.4.1.1) that deep water oxygen depletions are particularly stressful to mussels in these environments.

#### 6.5.3.2 Between waterbodies

As for comparison of size distributions between billabongs, nonselective sampling in Georgetown, Mudginberri, Buffalo and Nankeen billabongs biases the age structures of their mussel populations. This bias as argued in section 6.5.2.2 is minor considering the rapid growth of juveniles and is assumed to have no major and significant effect on mean age of the populations. These comments are made even more relevant when it is considered that for 1981 and 1982 when sampling was most concentrated, recruitment in fact was relatively poor in those billabongs where young mussels may have been missed (section 6.6.2). An exception to this rule, however, are the populations in the Magela Creek channel in which there is apparently regular year-to-year recruitment. Thus, recruitment and collection biases were not large enough to adversely affect comparisons between waterbodies.

Mean ages, their standard deviations, maximum and minimum ages and sample sizes of aged mussels from the Magela Creek waterbodies are shown in Table 6.37. Figures 6.28 and 6.29 show the age frequency distributions of mussels from the various waterbodies in relation to the year of recruitment of the particular age classes. A feature of these figures (also from Table 6.37), is the considerable variation in life-spans between populations of mussels. Whilst longevity and mortality are discussed elsewhere (section 6.7), a general observation is that populations are long-lived, indicating low adult mortality. The age distributions (accounting for age, classed according to year

of recruitment) of populations from some waterbodies show a gradual decrease in numbers from the youngest age class to the oldest, indicating regular year-to-year recruitment. This is a feature of the Georgetown billabong population, and is also shown for the Magela Creek channel, although the very young age classes were inadequately sampled. Although dominant year classes are present in the Mudginberri and Buffalo mussel populations, the gradual decline in numbers over the lifespan suggests that recruitment is fairly regular. Irregular age distributions characterised the populations in other billabongs signifying irregular, and in most cases, considerable, year to year variation in recruitment, or occasionally significant adult mortality.

Bell-shaped age distributions are thought to typify stable populations and where the bell is skewed to the left, the populations can be regarded as increasing and virile. When mean age is compared to maximum age in the mussel populations of the Magela Creek (Table 6.37), it is always much less than half the value of the latter. Thus these populations may be thought of as young and increasing. For most mussel populations studied elsewhere, the typical bell-shaped nature of their age distributions is explained by an absence of the youngest age classes. However, irregularity rather than a bell-shaped nature characterised the age distributions of populations in the present study, and young were present in all numbers from abundant to scarce. If young were uncommon, it was because they were inadequately sampled or recruitment (for reasons governed by the prevailing environmental conditions, section 6.6.2) was poor over the relevant periods of the study. There was no evidence that young were scarce because they

occupied a habitat remote from that of the adults (section 6.6.1). Thus despite some 'typical' appearances ascribed to the age frequency distributions of freshwater mussels and the very general interpretations given to their shapes, an ecological basis for the variation and irregularity in some age distributions of mussel populations in the Magela Creek can be ascribed in a quantitative manner to environmental factors that affect both recruitment and mortality. Using the population age distributions as portrayed in Figures 6.28 and 6.29, the following two sections pertaining to recruitment and mortality explain how these age structures are modified by the factors that determine recruitment and death rates.

#### 6.6 Recruitment of metamorphosed juveniles

##### 6.6.1 Seasonal and spatial occurrence

###### Seasonal occurrence

Non-selective sampling of mussels in the Magela Creek was carried out in four billabongs (section 3.2.1). Monthly length-frequency distributions for the populations in three of the billabongs, Georgetown, Mudginberri and Nankeen, are shown in Figures 6.2-6.4. Generally, only Wet season conditions provide the clean, well oxygenated waters needed for growth and development of the newly metamorphosed juvenile. These requirements are reflected in the seasonal nature of recruitment of mussels in the billabongs (Figs 6.2-6.4).

Juvenile mussels in Georgetown billabong are recruited in the shallows during the Wet to mid-Dry - that is, from February to as late as August (Fig. 6.2). The relatively protracted period of settlement of young mussels here, reflects the provision of clean, aerated waters in the littoral zones over this period. Later in the Dry, the extremely turbid waters are inhibitive to larval production and presumably to larval development. It is likely too, that significant mortality of juveniles that settle late in the recruitment period occurs from the high amounts of suspended solids. These might be expected to interfere with normal gill functioning of the sensitive young mussel. Thus, distinct juvenile modes progress through the late Dry showing the clear seasonality of recruitment (Fig. 6.2).

Significant recruitment in Mudginberri occurs when Wet season flow is discernible through the billabong between January and May (Fig. 6.3). Dissolved oxygen concentrations are highest in the billabong at these times (Fig. 2.20). In the relatively deep waters otherwise, even the slightly depressed levels of oxygen during the Dry are apparently sufficiently stressful to prevent larval settlement and development. This might be readily understood for the silty and organic sediments of the deepest parts of the billabong where microhabitat oxygen availability is likely to be relatively low and where silt may clog the gills of the young. Some minimal recruitment occurred, however, throughout the Dry season in Mudginberri (Fig. 6.3). This was observed mostly at site 2 (Figure 3.1) where waters are shallower and the sediments less organic and silty than elsewhere. Juveniles could also be found on sandy littoral areas at the southern end of the billabong in the late Dry. These sites are presumably better aerated

than elsewhere. However, the juvenile length-frequency modes that occur in the mid to late Dry do not progress, and so mortality of the small Dry season recruits appears to be high. Fish predation may be more intense in the clean waters of the Dry, or periodic lulls in oxygen availability that accompany the cycles of algal blooms in the billabong later in the Dry (section 2.3.2.2) may be destructive.

Recruitment in the floodplain billabongs is probably the most seasonal and synchronised for the waterbodies as dissolved oxygen is of sufficiently high concentration and turbidity generally minimal only during the Wet season. Newly recruited mussels were observed in Nankeen billabong between February and May (Fig. 6.4). Severe oxygen depletions that accompany the Wet-Dry interchange (section 2.3.2.2) prevent larval settlement in the mid Dry in Nankeen and presumably the other floodplain billabongs. Although oxygen concentrations may be relatively high in the mid to late Dry, the high turbidity observed in Nankeen at these times, inhibits larval production and subsequent recruitment. Dissolved oxygen concentrations in the clean, late Dry season waters of Island and Leichhardt billabongs are probably not sufficiently high enough for significant recruitment then. Both deepwater oxygen depletion and turbidity are likely to prevent Dry season recruitment in the heavily vegetated backflow billabongs, Gulungul and Corndorl as well. It is conceivable however, that in well oxygenated littoral zones as in Georgetown, some recruitment might occur well into the Dry in either billabong. In at least Gulungul billabong, however, flooded littoral regions have an unsuitable bottom sediment of hard-packed clay. In any case, waters may recede too rapidly over the broad shallow basin for juveniles to



retreat in time to deeper waters.

As a general rule then, mussels are recruited seasonally into the Magela Creek waterbodies in a relatively short period for respective populations, within the broader time span of the beginning of the Wet to the mid Dry.

#### Spatial occurrence

Tables 6.38-6.40 show the numbers of juvenile, young-of-year mussels quantitatively sampled in Mudginberri, Buffalo and Nankeen billabongs respectively, in relation to both adults sampled and habitat. Chi-squared tests were used to discern differences in the proportions of juveniles in relation to adults in the different habitats. Such differences might indicate different habitat requirements of the young.

A graphic representation of recruitment patterns was chosen for Georgetown billabong (Fig. 6.30). Shown in this figure is the population structure of mussels during 1981, along the shallow, relatively sandy transect upstream in the billabong. Newly recruited mussels (< 20 mm in size) appear from May to about August in the shallow reaches of the transect, moving progressively to deeper regions as the waters recede. The recruitment pattern was not as pronounced on the northern shore of the transect (Fig. 6.30), nor on the deeper, muddy transect downstream. This is explained partly because the inundated shallows of these regions were steep and not very extensive, and/or the bottom types comprised mostly unsuitable,

hard-packed mud. The occurrence of juveniles in the shallows is almost certainly related to the habits of the host fishes that were notably active amongst the weeded littoral zones at the time of juvenile mussel recruitment. It is conceivable that some additional deepwater oxygen depletions may also have restricted settlement elsewhere over this period.

Chi-squared tests revealed highly significant differences ( $\chi^2 = 108.8$ ,  $P < 0.001$ ) among the different sites sampled in Mudginberri, and no significant differences ( $\chi^2 = 12.41$ ,  $P > 0.05$ ) in Buffalo billabong, in the proportions of young relative to adults. Strong currents flow through Mudginberri billabong, and the distribution of juveniles might therefore be expected to be influenced considerably by flow patterns. More juvenile mussels were found at site 3 than might be expected, while fewer were found at sites 1 and 5 (Table 6.38). Particularly high flooding occurred in February 1980 and March 1981 that may have been responsible for sweeping juveniles away from sites 1 and 5 where currents would be expected to be stronger in relation to other sites (Fig. 2.15). Site 3 is a backwater area into which juveniles are probably swept during high discharge events, and might be expected to record relatively larger numbers of juveniles. The silty and organic sediments here may nevertheless be the cause of significantly higher mortality of juveniles over the ensuing Dry if the site receives flood refugees on a regular annual basis. By contrast, currents through Buffalo billabong during the Wet are considerably reduced, and the young are notably evenly dispersed over the billabong (Table 6.39). The sandy sites, 1 and 8, can be expected to receive stronger currents during the Wet. The number of juveniles on these sites is relatively

low (Table 6.39) but is proportionately the same as adults. Also stream currents or other factors may modify the distributional patterns of the host fishes in the channel billabongs. The high densities of mussels in the soft clay sediments of both billabongs for example (Tables 5.4 and 5.5) may be related to their location in eddies to the side of vigorous stream flow. These places may be expected to be frequented by feeding or migrating fishes (section 2.3.3). The backwater site (3) in Mudginberri billabong might also be frequented more by feeding fishes than elsewhere.

When data were grouped according to five depth zones in Nankeen (0.0-0.49; 0.5-0.99; 1.0-1.49; 1.5-1.99; 2.0-2.49 m), highly significant differences were found in the proportions of young to adults, among the different depths ( $\chi^2 = 35.7$ ,  $P < 0.001$ ). When the proportions of young relative to adults were plotted against increasing depth, the proportion declined with depth (Fig. 6.31). A significant ( $P < 0.05$ ) negative exponential regression equation was found to describe the relationship, shown in Figure 6.31. (The percentages of the dependent variable were transformed using a complementary log-log function as described in section 6.6.2). Thus from this Figure, and from earlier data (section 6.5.3.1), the occurrence of juveniles differs significantly from the adults, and recruitment is highest in the shallows. The marginal waters of the floodplain billabongs are reasonably well vegetated during the Wet, a feature that apparently attracts fish to the shallows. The occurrence of juvenile mussels in the shallows therefore is presumably related to the same distribution of their hosts. Further, deepwater oxygen depletions which juveniles are particularly susceptible to,

undoubtedly restrict the young to the shallows either through causing higher mortality of young at depth or by stimulating movement away from the depths.

Thus in billabongs with shallow shelving banks, juveniles occur in different habitats than those of the adults. Occurrence in the shallower waters is presumably related to the habits of the host fishes, and the higher oxygen concentrations that occur there. Otherwise, differences between juvenile and adult occurrence appear to be related to dispersal by stream currents, and conceivably by the influence of that factor upon local fish habits and locations. None of the observed differences in habitat of juveniles and adults could be attributed to the need by juveniles of quite specific sediment types. Young were common in soft, crumbly mud and detritus in Georgetown, fine silt and clay in Nankeen (homogeneous at all depths) and from sand, grading to organic and silty soft sediments in backwater regions, of Mudginberri and Buffalo billabongs. These sediments range widely in texture and consistency, and possibly the least suitable are those silty sediments in the backwater regions of the channel billabongs. On these sediments of site 3 of Mudginberri billabong, however, are recorded the highest proportion of juveniles to adults of any other site, and within any other billabong (Tables 6.38 - 6.40).

#### 6.6.2. Factors affecting recruitment

The occurrence of recruitment during the Wet, and earlier evidence (section 5.4.1.2), strongly implicate Wet season flow as an important

determinant of juvenile recruitment in, at least, billabongs lying on the mainstream channel of the Magela Creek. As a supplier of dissolved oxygen, Wet season discharge is especially critical to populations within the heavily vegetated, floodplain billabongs where minimal or intermittent flow under the prevailing, warm conditions of the Wet, quickly produces deoxygenating conditions. Low dissolved oxygen concentrations (as mentioned earlier, section 5.4.1.2.2) are inhibitive to larval production in female mussels, and detrimental to newly-recruited juveniles. From Figure 6.29, a number of dominant year classes are apparent in the age structures of mussel populations in the floodplain billabongs. The peak in year class strength occurs in mussels recruited during either the 1973/1974 or 1974/1975 Wet seasons. Discharge data available for the gauging station below Jabiru (GS 821009, Fig. 2.3), show a number of wet years at about these times.

As observed in the floodplain billabongs, the Wet/Dry interchange is a period of regular, and often severe oxygen depletion. This period therefore might be expected to be critical for juvenile survival. If the Wet season were to end early, a relatively large period of warm weather remains until the cooler period (commencing in about May) under which deoxygenating conditions may be more pronounced. If Wet season flow were to continue relatively late into the season, only a short period of warm weather would remain before the cooler nights of the Dry effectively mix the water column, breaking down stratification and reducing periods of anoxia. Further, a protracted and late finish to the Wet not only means a longer breeding season and enhanced recruitment, but also provides a longer growing season for the

juvenile. From experimental observations (Appendix 6), tolerance to anoxia increases with increasing mussel size, and so the larger the juveniles are in size at the end of the Wet, presumably the better are their chances of survival when deoxygenating conditions begin. Thus, the most dominant year class in the floodplain billabongs originates from the 1974/1975 Wet season (Fig. 6.29). This Wet was not the highest in terms of total discharge, but significantly, the April discharge was the highest (Fig. 2.3) and so the late finish to the Wet may presumably have enhanced recruitment for the reasons mentioned above. It is also significant that this dominant year class occurred in Island, Leichhardt and Jabiluka billabongs, where anoxia at the Wet/Dry interchange is most pronounced (Fig. 2.21). A limitation to this correlative approach, however, is that Dry season oxygen concentrations are presumably also responsible for post-recruitment survival. Information as to when the Wet season finishes gives by no means complete prediction of the oxygen relations in billabongs that are likely to prevail throughout the ensuing Dry.

Regression analysis was used to test for correlations between discharge and recruitment in the floodplain billabongs. Although a gauging station is located on the floodplain at Jabiluka billabong (GS 821017), records held are not extensive, and because of the complexity of flow patterns on the floodplain, reliable rating and gauging by the station is not as yet guaranteed (N.T. Dept. Transport and Works, Water Division, 1979). More extensive and reliable records, however, are held for the gauging station upstream near Jabiru (GS 821009). For the limited and reliable data that is available, a good correlation of discharge exists between the two gauging stations (N.T.

Dept. Transport and Works, Water Division, 1980). (It is notable, however, that flow begins earlier and ceases earlier at Jabiru than on the floodplain at Jabiluka.) Monthly discharge data for the 9 year period from the 1971/1972 to the 1979/1980 Wet season from the gauging station below Jabiru were used in the analyses. Because of the similarity in age structure between mussel populations in all of the floodplain billabongs (Fig. 6.29), the year class data were combined. Strength of year class for each billabong, was calculated as a proportion of the total numbers of mussels of all the age classes recruited over the 9 year period that discharge records had been kept. An averaged proportion was then calculated for each year class, for the floodplain billabongs. It is conceded, however, that the regression analysis used would result to some degree in crude and inaccurate correlations, as the error introduced because of natural mortality effects was not considered. Although mortality in one floodplain billabong (Nankeen), over the 9 year period of life considered here, amounted to less than 10 percent (Fig. 6.36), this value is probably higher in billabongs where anoxic periods (likely to be a significant cause of mortality, section 6.7.3) are more severe, such as in Leichhardt billabong.

Systematically, various discharge combinations were regressed against year class strength (the latter arcsine transformed). Total discharge for the Wet season for instance, may not be so meaningful if most of the flow occurred in one relatively short period that did not leave time for either larval production, the parasitic phase or sufficient growth before the effects of deoxygenation at the end of the Wet were felt. A critical two or three month period of the Wet for example,

may be all that is required to effectively determine recruitment. Thus, discharge was tested one month at a time (e.g. December discharge against strength of year class, January discharge against strength of year class, etc.), then discharge combined for two month periods, and so on, discharge adding cumulatively until total discharge was regressed against year class strength. The final test used was a multiple regression analysis, regressing all months, December to May for the 9 year period of discharge data against recruitment.

As shown in Table 6.41, many significant correlations ( $P < 0.05$ ) were found between discharge and year class strength. (A few of the plots indicated that an exponential model may have provided a slightly better fit to the data. However, with the exception of the equation described below, these were not calculated.) It is notable that the latter months of the Wet are heavily represented in the regressions, especially where combined periods of discharge were shortest. This adds strong supportive evidence to the claim that late Wet season flow is most critical to juvenile recruitment and subsequent survival. While a few discharge periods bore stronger correlations to year class strength over others ( $P < 0.01$ ), no one correlation was outstanding. For descriptive purposes, an adequate model nevertheless was considered to be that regression equation combining all of the significant discharge that might be felt through the floodplain billabongs, namely the period January to May. (From discharge data at Jabiluka, significant stream flow begins in January and extends well into May, whereas upstream at GS 821009, flow is not nearly as discernible during May.) The linear regression equation for this



period is described in Table 6.41. An exponential model, however, shown in Figure 6.32 provided a better fit to the data ( $P < 0.01$ ). The model was derived by transforming the percentages of the dependent variable with a complementary log-log function,  $\log(-\log(1-Y/100))$ . The regression equation is:

$$Y = 100(1 - \text{EXP}(-0.043\text{EXP}(0.00234X))) \quad (P < 0.01, r^2 = 0.653)$$

where  $Y$  = year class strength (percent)

and  $X$  = total discharge for the period January to May  
( $\text{m}^3 \times 10^{-6}$ ).

Hence, total discharge between January and May accounted for 65 percent of the variation in year class strength of mussels in the floodplain billabongs over the 9 year period of discharge records.

The best fit of the linear multiple regression equation, however, accounted for all (100%) of the variance in year class strength. The multiple regression equation is:

$$Y = 0.178 - 0.0017X_1 + 0.0012X_2 + 0.0004X_3 + 0.0011X_4 - 0.0017X_5 + 0.002X_6 \quad (r^2 = 1.000)$$

where  $Y$  = Year class strength (arcsin  $\sqrt{Y}$  in percent/100),  
radians)

$X_1$  = December,

$X_2$  = January,

$X_3$  = March,

$X_4$  = April,

$X_5$  = May.

$X_6$  = June discharge ( $m^3 \times 10^{-6}$ ).

Table 6.42 shows the significance levels of the regression variables. December, January, March and April discharge are important variables. April discharge is by far the most important variable (Students  $t = 82.05$ ) followed by March and January (Table 6.42). Thus, it is predicted that late Wet season discharge (March and April) enhances recruitment. Discharge, however, at the extremities of the Wet (December and May) has a negative effect on recruitment. (The negative sign is uninterpretable.) Nevertheless, the sign and significance levels of the January, March and April variables are more easily interpreted. High January discharge (the first significant flushing that the floodplain billabongs receive) presumably results in early juvenile metamorphosis and settlement. While February discharge is almost always greater than in January (Fig. 2.3) high discharge in March and April further enhances recruitment and lengthens the growing season of those mussels recruited as early as January. Thus by the end of the Wet, early recruits may be of considerable size, and the late finish of the season might nevertheless shorten the period that the young are exposed to low dissolved oxygen environments.

The shorter period of time over which mussels were sampled, and the bias against the small juveniles in the collections precluded analysis of the 1980/1981 and 1981/1982 Wet season recruits. The multiple regression equation, however, predicted relatively good recruitment in the 1980/1981 Wet (about half the strength of the most dominant (1974/1975) year class) but only about half this value again for the strength of the 1981/1982 Wet season year class. Early indications from Nankeen billabong at least, where non-selective sampling was

performed, are that these values may in fact be quite accurate. Hence the multiple regression equation as it stands appears to be an adequate model, having significant predictive value. Further discharge data and information on mussel age structure in the floodplain billabongs will presumably increase the predictive value of the model. The generalised model, moreover, could be recalculated using data from individual billabongs, so that recruitment might then be predicted for specific floodplain billabongs.

From Figure 6.28, it is apparent that recruitment in Corndorl billabong follows the same year to year pattern as in the floodplain billabongs. Presumably this reflects the fact that this heavily vegetated billabong behaves in a similar fashion to the floodplain billabongs at the end of the Wet, with periods of deoxygenation (section 2.3.2.2). Therefore, protracted or extended Wet seasons also enhance recruitment here and similar correlations can be assumed. In the channel billabongs, Mudginberri and Buffalo, recruitment is much more regular, with much slighter evidence that high discharge and extended Wet seasons benefit recruitment. Presumably this reflects the observation that neither billabong becomes significantly deoxygenated at the Wet/Dry interchange, and survival of recruits therefore, is less dependent upon the amount of water discharged through the billabong during the Wet. Even in the Magela Creek channel where recruitment is very regular, the beneficial effects of the extended 1974/1975 are felt in the slightly elevated age class peak in the population (Fig. 6.28). Dominant age classes in Gulungul billabong finally, may be more influenced by remaining waters left in the billabong at the end of the Dry, than by Wet season discharge

patterns themselves. Significant mortality of mussels might be expected if the billabong were to dry out. Further discussion about the age structure of this population therefore, is dealt with in section 6.7.3.

## 6.7 Mortality

### 6.7.1 Survival between the sexes

Plots of sex ratios with age were made to discern whether at any stage in the lifespan of mussels within particular waterbodies, differential mortality occurred. From the plots, it was clearly apparent that sex ratios of Velesunio angasi within several billabongs, changed with increasing age. The relationships are shown for these populations in Figure 6.33. In billabongs where changing sex ratios were observed, invariably the proportion of females appeared to decline, at least in the latter years of life (Fig. 6.33). Regression analysis was performed using sex ratio and weighted age data of the oldest age classes, systematically including younger age classes until the correlation became insignificant ( $P > 0.05$ ). From the next age class onward therefore, it could be said that the proportion of females significantly declined with age. Such relationships were found in mussel populations in Mudginberri, Island, JaJa and Leichhardt billabongs. The same regression approach was used for the data from Jabiluka billabong, but in reverse order, in which the proportion of females significantly increased with age (Fig. 6.33). The linear regression equations and the range of ages over which significant correlations between sex ratio and age were found ( $P < 0.05$ ), are

shown in Table 6.43.

While the age variations observed in the sex structure of mussel populations might indicate differential mortality of the sexes, other interpretations are available. Tudorancea (1969) indicated that the variations in sex ratios of freshwater mussels arose from sex transformation with age. He found more male Unio tumidus both at younger and older ages, while females outnumbered males in the middle years. While no significant quadratic effects could be found using individual observations of sex ratio and age, nevertheless the same trend as found by Tudorancea is apparent in the sex ratios observed throughout the lifespans of mussel populations in some Magela Creek billabongs (Fig. 6.33).

The notion of major sex transformations occurring within the lifespan of V. angasi is considered in section 7.5, but it is of interest to this discussion that the proportions of females in some billabongs decline at older ages. It might be expected that associated with the approach of old age in organisms, are a physiological weakening and increasing intolerance to environmental stresses. It is worth noting that the populations in which the numbers of females decline with old age in the Magela Creek, are mostly from the floodplain billabongs where a common major stress is their poor oxygen relations. Whether the decline in the numbers of females at older ages is due to either a sex transformation, higher mortality with increasing age, or both, it is tempting to suggest that of either sex, the females might be expected to be more stressed at age. Higher demands are presumably placed upon the physiology of female mussels because the gills serve

an additional function of harbouring and nurturing the larvae. In low oxygen environments therefore, older female mussels may be hard pressed to find sufficient oxygen and yet perform the additional gill functions of feeding and larval brooding. In fact, at low environmental oxygen levels, larval production by female mussels in the Magela Creek billabongs is inhibited (section 7.10.1). Thus as a sexual strategy, reproductive effort might be optimised at older ages in environments with poor oxygen relations, by production of male gametes. Alternatively or additionally, because females may be more vulnerable to stresses at old age, their lifespan might be expected to be considerably shortened. The latter interpretation is strongly suspected (sections 7.5 and 7.6).

#### 6.7.2. Estimation of survival rates

Because quantitative samples were taken systematically over a two year period of collecting, opportunities were available to estimate age specific mortality in mussel populations from Georgetown, Mudginberri and Nankeen billabongs. Age specific mortalities are of considerable interest in population studies because as mortality usually varies greatly with age, is then possible to elucidate the forces underlying the crude, overall population mortality (Odum, 1971). For freshwater mussel populations, age specific mortality rates have been estimated for populations of Margaritifera margaritifera (Bauer, 1983) and Anodonta anatina (Negus, 1966). Bauer's (1983) estimates were based upon ratios of living mussels in every age class and numbers of empty shells, while Negus (1966) compared the proportions of mussels within specific age classes, between successive years for her estimates.

Otherwise, both Haukioja and Hakala (1978b) and Green (1980) estimated the mortality of the oldest part of certain Anodonta populations, by analysis of catch curves.

In the present study, both catch curve analysis and ratios of mussel numbers in specific age classes, between successive years were used to estimate age specific mortality. All mussels collected from the routine monthly samples in Georgetown, Mudginberri and Nankeen billabongs were used in the analyses. A proportion of the samples of adult mussels from Georgetown and Mudginberri billabongs were unaged (section 3.3). The mussels belonging to this proportion were assigned an age according to the overall proportions of adult age classes estimated earlier (section 6.5.3.2). Age frequency distributions were then constructed for the three populations, pooling numbers of mussels within specific age classes collected over the two year period, without regard for the year of recruitment. Thus, young of year mussels ('0' years, Fig. 6.34) comprised 1980, 1981 and 1982 recruits and so on; no year class therefore was biased by the shorter or longer period of collecting. The age distributions are shown in Fig. 6.34.

From Figure 6.34, it is clear that recruitment in Georgetown billabong is fairly constant and the age frequency distributions show a gradual decrease in numbers with increasing age. Mortality rate in this population therefore could be estimated from catch curve analysis (Ricker, 1958). By this method, the natural log of mussel numbers is regressed against age. Mortality rate ( $M$ ) which is constant over all age classes, is found from the slope ( $b$ ) of the resulting negative

linear regression, by means of the equation:

$$(m = 1.0 - e^{\mu y})$$

Recruitment in Mudginberri and Nankeen billabongs was less regular, and the method of Negus (1966) was used to estimate age specific mortalities. Survival was estimated by comparing the numbers of one age class collected in the second year to those of the same cohort collected in the previous year. For example, survival at the end of the first year of life was found from the ratio:

$$\frac{\text{Number of 1-year-olds in 1981/1982}}{\text{Number of 0-year-olds in 1980/1981}}$$

, each year represented by the period June to May inclusive. The resulting ratios were plotted with increasing age and a line fitted by eye to predict annual survival rate for each age class (Fig. 6.35). Both small sample numbers and inaccurate age determinations precluded the estimation of survival rates for the final 11 years of life of mussels in Mudginberri billabong by this method. Catch curve analysis therefore was used for this oldest portion of the population, in which mortality is estimated from the slope of the semi-log regression between mussel numbers and age as described above. Although this method assumes that recruitment is regular and mortality constant in the population concerned, year to year fluctuations in recruitment in Mudginberri billabong are fairly slight (Fig. 6.28) while mortality nevertheless appears to approach a constancy at greater ages, from the trend apparent in the survival values of the ages immediately preceding (Fig. 6.35). Instantaneous mortality rates were calculated according to the relationship:

$$S = (1.0 - M) = e^{-\mu}$$

where S = annual survival rate,



M = annual mortality rate,

Z = instantaneous mortality rate.

The values for age specific annual survival rates and instantaneous mortality rates of mussel populations in Mudginberri and Nankeen billabongs are shown in Table 6.44. Using these smoothed data and the mortality rate estimated for the Georgetown population (see below), survivorship curves were drawn for the three populations, where survival is plotted against age, under the conditions of regular year-to-year recruitment (Fig. 6.36).

The negative exponential equation relating mussel numbers and age for the Georgetown population was calculated to be:

$$Y = 1735e^{-0.286x} \quad (r^2 = 0.825, P < 0.001)$$

where Y = numbers of mussels

and X = age in years.

From this relationship, the annual mortality rate (M) was found to be 24.9 percent, and the instantaneous mortality rate therefore, 0.29. If recruitment were regular, the age structure of the mussel populations in Georgetown, Mudginberri and Nankeen billabongs would appear as shown in Figure 6.36. (An implicit assumption in drawing up the survivorship curves shown in Fig. 6.36, is that survival found between successive year classes of mussels collected over the present two year study period, has been the persistent pattern in time.) The concave curve of the Georgetown mussel population indicates a constant specific rate of mortality over the entire life span. The populations in Mudginberri and Nankeen billabongs, however, display "stair-step"

types of survivorship curves (Odum, 1971), where survival undergoes sharp changes between different age groups. Both populations harbour intermediate age classes in which mortality is insignificant. This high survival phase is most pronounced in Mudginberri billabong where it extends for some 10 years. In both Mudginberri and Nankeen billabong populations, however, mortality is highest in the earlier and older age classes (Fig. 6.36). Further discussion of these curves in relation to mortality causes is made in the following section.

### 6.7.3 Mortality causes and longevity

Some causes of mortality of freshwater mussels in waterbodies of the Magela Creek have previously been mentioned or suggested, in a general manner in Chapter 5. Further information regarding these and other factors is presented here. Predation, drought, flooding and anoxia are believed to be the main causes of mortality of Velesunio angasi in the Magela Creek.

Little information and circumstantial evidence was gained over the period of the study as to the chief predators of freshwater mussels in the Region. Aboriginal man both in the past and present is a very significant predator of mussels from shallow waters over the Dry season. In the Magela Creek, evidence of his collecting activities (via observations or shell middens) was found in the braided Magela Creek channel in the early Dry, and later in the season, in Georgetown, Corndorl, Mudginberri and Buffalo billabongs. The pattern of incision marks on shell fragments in other middens, was identical to the description by Fisher (1973) for predation by water rats

(Hydromys) in southern Australia. Significant Dry season predation by water rats was observed in shallow billabongs, and was especially evident at the Wet-Dry interchange in the Magela Creek channel above Mudginberri. Shell fragments have been found in the stomachs of turtles in the Region, and mussels form a major component of the diet of certain populations of one species in particular, Emydura australis, and to a lesser extent in Carettochelys insculpta (J. Legler, pers. comm.). Otherwise, mussels are almost certainly preyed upon heavily in the juvenile stages by fish, and shell fragments at least, have been observed in the stomachs of certain catfishes: Hexanematichthys leptaspis; H. australis; and Neosilurus sp. (Bishop et al., 1981). Juvenile mussels have been found among the stomach contents of Glossy Ibis (Plegadis falcinellus, P. Dostine, pers. comm.). Similarly, White Ibis (Threskiornis molucca), observed feeding in the shallows of Georgetown billabong, were strongly suspected of taking juvenile mussels that were present here in large numbers during the mid Dry season (Fig. 6.30). This bird species has also been noted to prey upon mussels in southeastern Australia (Vestjens, 1973).

Prolonged Dry seasons presumably, are a major factor in explaining the general absence of mussels from shallow backflow billabongs. The direct causes of mortality may be increased predation and high water temperatures in the shallow waters remaining at the end of the Dry or from direct exposure and desiccation if the waters dry up completely. From accompanying experimental studies, V. angasi tolerated temperatures above 45° C before 50 percent of the population succumbed, and adults survived out of water (but indoors and away from direct exposure to sunlight) for several months. Juveniles, however, are

less tolerant of dehydration. Accompanying outdoor experiments also showed that mussels reacted to falling water levels by burrowing, thereby avoiding the effects of high water temperatures in the surrounding shallow waters. However, in sediments where mussels cannot burrow, high water temperatures and exposure to sunlight were fatal. Burrowing in sandy sediments is also of little survival value as the poor insulative properties of sand provide little protection from high ambient temperatures. Mussels that burrow in muddy sediments increase their chances of survival, but cracks that appear in drying mud nevertheless expose a proportion of mussels to either the lethal effects of dehydration or direct sunlight.

Young of year mussels might be expected to be particularly vulnerable in a shallow backflow billabong such as Gulungul after a prolonged Dry season. Three age classes dominate the age distributions of the mussel population in Gulungul billabong: those derived from the Wet seasons of 1972/1973, 1973/1974 and 1980/1981 (Fig. 6.28). Gauge height data for the billabong are unavailable for these periods, but discharge data are available for the period 1971 to 1979 in the small, feeder stream (Gulungul Creek) upstream of the billabong (GS 821012, N.T. Dept. Transport and Works, Water Division, 1980). Presumably these data give some indication as to how early the billabong begins to fill with Wet season waters and how late in the Wet water is discharged into the billabong. Early filling of the billabong in particular (say, November), is assumed to mean that the billabong did not dry out in that particular year. The months of late and early Dry season discharge into the billabong (May, June, November and December) were regressed against year class strength of mussels (Fig. 6.28).

(The percentages of the dependent variable were arcsine transformed.) November discharge only was significantly correlated with year class strength according to the linear regression equation:

$$Y = 0.218 + 0.525X \quad (r^2 = 0.659, P < 0.05)$$

where Y = year class strength over the relevant period ( $\arcsin \sqrt{Y}$  in percent/100), radians)

X = total discharge at gauging station 821012 during November ( $m^3 \times 10^{-6}$ ).

This result indicates that juvenile survival is enhanced in those years in which Gulungul billabong does not dry out significantly. The 1980/1981 year class was not included in the regressions because of the lack of discharge data. The billabong, however, did not dry up and depth by the end of 1981 still averaged 0.3 m (Table 2.1), a year in which juveniles were also quite common (Fig. 6.28). Better prediction of year class strength in Gulungul billabong might be achieved when billabong gauge height data replace stream discharges, as water levels in the billabong may not necessarily strongly correlate with discharge upstream of the billabong.

Flooding has been mentioned as a significant factor affecting mussel distribution and abundance in some billabongs of the Magela Creek (section 5.4.1.2.1). Flood events preclude habitation on sandy sediments in particular waterbodies, and in Georgetown billabong at least, were responsible for large scale displacement of mussels (section 5.4.1.2.1). The mussels that were swept downstream of the billabong, succumbed either to intolerably high water temperatures or air temperatures as the shallow waters about them retreated.

Juvenile mussels are particularly sensitive to low dissolved oxygen concentrations (Appendix 6), an observation already strongly implicated in recruitment success or failure in particular billabongs of the Magela Creek (section 6.6.2). There is little evidence, however, that the periods of low dissolved oxygen concentration observed in the floodplain billabongs are severe and stressful enough to cause mass mortality of adult mussels at these times. No mussel kills were observed that could be attributed to the direct effects of anoxia during the seasonal declines in dissolved oxygen in the billabongs. From experimental observations, adult mussels in fact may survive for prolonged periods (months) without oxygen (Appendix 6). It is conceivable nevertheless, that the cumulative effect of seasonal dissolved oxygen depletion over periods of years, may prove stressful enough to weaken the physiological tolerance of adult mussels and thus perhaps shorten the lifespan of mussels in the environments prone to these conditions. Whether the mussel kills that accompany fish kills at the Dry-Wet interchange (section 5.5), are significant factors in explaining mortality in the floodplain billabongs, is uncertain. The low numbers of dead mussels observed on one of these occasions in Leichhardt billabong at least, indicate that the effects are not severe, but the stressful factor, like anoxia, may conceivably weaken the tolerances of mussels.

In the light of knowledge of observed or likely causes of mortality of mussels, the age structure of mussel populations (Fig. 6.28 and 6.29), longevities (Table 6.37) and age specific mortalities (Fig. 6.36), the factors underlying the overall population mortality in waterbodies may now be better understood:

In the shallow backflow billabong of Georgetown, mortality is constant over all age classes (Fig. 6.36). Late Dry season stresses presumably account for much of the loss in mussel numbers from year to year. These stresses include: high turbidities and associated low food availability; high water temperatures and dehydration if water subsidence is particularly rapid; and increased mammalian predation. Flood events during the Wet presumably account for regular loss of mussels when these are physically displaced from the billabong (section 5.4.1.2.1). All age classes nevertheless are equally vulnerable to mortality by whatever cause.

No evidence was found of avian and mammalian predation in Nankeen, nor any other floodplain billabong, but turbidity and low food availability may be possible causes of mortality during the late Dry. Unlike Georgetown, mortality is low in Nankeen for mussels of younger ages between 3 and 5 years (Fig. 6.36). Whatever the causes of mortality in the billabong, these age classes therefore are the most tolerant and vigorous. The very youngest and older age classes of the population suffer highest mortality. The youngest age classes may be expected to be preyed upon more heavily than other age classes. As shown later, low dissolved oxygen concentrations are probably major causes of mortality of mussels in the Magela Creek billabongs. The effects of course are most pronounced in the floodplain billabongs where the youngest and perhaps oldest age classes of mussels may be least tolerant to their effects.

The environment in Mudginberri billabong, however, is apparently a

most favourable one for mussels. Water quality is particularly equitable year round, with waters remaining clean, well oxygenated and adequately supplied with food. The deeper waters of the billabong moreover ensure that mammalian predation at least is relatively low. Thus, mussels in this billabong (and in Buffalo billabong for which these comments may also apply) are the longest-lived, and for a period of some ten years in the intermediate ages no discernible mortality is apparent (Fig. 6.36). Predation is almost certainly intense in the youngest years, and perhaps to some degree in the oldest age classes as well. Senescence, presumably, accounts for much of the increase in mortality at greater ages.

Longevity varies widely between mussel populations of different waterbodies (Table 6.37). Drought and dehydration may be factors that determine the maximum ages of mussels in Gulungul billabong and the ephemeral Magela Creek channel. Otherwise, dissolved oxygen appears to be at least one important factor that determines longevity of mussels in billabongs which presumably never dry out completely. A significant correlation was found between mean, dissolved oxygen concentration of billabongs and the maximum ages of mussels ( $P < 0.05$ ). The linear regression equation is described and plotted in Figure 6.37. Because they affect maximum ages attained, dissolved oxygen concentrations in billabongs presumably have considerable influence upon the mortality of at least the oldest proportion of the mussel populations. In billabongs where the concentrations are particularly low (e.g. Leichhardt), the effects of anoxia might be expected to act upon all the age classes. These results again (see Chapter 5) testify to the significance of dissolved oxygen conditions



in billabongs, to the general well being and development of mussel populations.

## 6.8 Movements

### 6.8.1 Lateral movements in a shallow backflow billabong.

Figure 6.30 shows the seasonal distribution of mussels in relation to location along the shallow, sandy transect sampled routinely in Georgetown billabong (Fig. 3.1). Movements were marked along this transect - particularly the southern end, as the sediments here are fairly soft and the slope of the banks fairly gentle. As seen from the figure, adult mussels (> 20 mm in size) move up onto the peripheral seasonally-inundated and weeded shallows during the Wet season. During the Wet and early Dry, juvenile mussels are recruited in these shallows (section 6.6.1) and both young and adults move back into deeper waters as the waters recede over the ensuing Dry.

The migration of adults onto the banks during the Wet season may be associated with feeding, reproduction or avoidance of the shifting sandy sediments of the central portions of the billabong. Faster growth rates were observed for adult mussels in the peripheral, shallow waters during the Wet (unpublished observations) indicating that food availability was higher in these reaches. Greater somatic growth and larval production might also be expected under these conditions. Further, as fish frequent the weeded shallows, the movements of mussels into these regions during the Wet therefore coincides with their distributional patterns, thus facilitating

parasitism of the fish by the glochidial larvae. Between the February and March samples (1981) floods displaced large numbers of mussels from the billabong (section 5.4.1.2.1). The central sandy reaches of the transect shown in Figure 6.30, are notably depauperate of mussels during March. Although some mussels may have been washed away from these central regions during the floods, nevertheless others apparently moved up or were washed onto the flooded banks over this time as both proportions and numbers of mussels were higher on the banks than at previous sampling occasions. Movements therefore, may be made in response to water movement. Receding water levels initiate a response to move to deeper water in avoidance of high water temperatures and exposure.

#### 6.8.2 Movements in a deep channel billabong

Of the some 8,000 mussels marked and released in Buffalo billabong, 591 of these were recovered twelve months later. 58 of the recovered mussels had moved beyond the 506 m<sup>2</sup> quadrats over which they were originally released. The movements in relation to numbers and direction in the billabong are shown in Figure 6.38. 17 of the movements occurred at the very southern end of the billabong, and were made in response to falling water levels during the late Dry season. The mussels were placed in shallow waters during May 1980 and moved to deeper waters as the sandy sediments became exposed during the Dry. Thus when these individual movements are discounted, 7.1 percent of the remaining recovered mussels had moved beyond the quadrats originally allocated them, for reasons other than receding water levels and imminent exposure.

The size of the quadrats over which mussels were released was designed to detect fairly large scale movements of mussels. The distances travelled into adjacent quadrats for example, could not be considered substantial as mussels initially released near the edge of a quadrat need only have moved a few metres at the most, to a new one. Thus, only two recoveries had moved sufficiently over the period for their movements to be termed significant. These movements occurred at the northern end of the billabong, over sandy sediments, and the shortest distances that the two mussels could possibly have moved were 50 and 70 metres respectively (Fig. 6.38). It is almost certain, however, that both movements occurred as a result of displacement downstream by wet season floods. The sandy sediments of the billabong were probably to some degree shifting during a large flood event in March 1981.

Chi squared tests were used to discern whether the movements throughout the billabong were random or not. Those movements involving responses to falling water levels were not included in the tests. An initial hypothesis to be tested was that the frequency of movements was the same in all four directions, north, south, east and west. Movements in a direction between two vectors were divided and apportioned equally to both directional vectors. Thus a northwest movement was considered half a north movement and half a westward movement. Very strong evidence was found against the hypothesis of random movement by mussels ( $\chi^2 = 27.44$ ,  $P < 0.001$ ). Tests were then conducted to discern whether northward movements were significantly more frequent than movements in other directions; whether southward movements were less frequent than movements either east or west; and

whether movements were equally frequent both east and westward. Northward movements were far more frequent than movements in any other direction ( $\chi^2 = 24.59$ ,  $P < 0.001$ ), and southward movements less frequent than movements either east or westward ( $\chi^2 = 4.59$ ,  $P < 0.05$ ). No differences were found in the frequencies of movements either east or westward ( $\chi^2 = 0.40$ ,  $P > 0.05$ ). Thus mussels moved predominantly northward or in a downstream direction, and moved least of all southward or upstream. No substrate related tests were conducted, but over half the movements (27 out of 41) were over sandy sediments.

Undoubtedly, the northward movement of mussels in the billabong was the result of a displacement downstream by a large flood event during March 1981, that rendered the sandy sediments of the billabong especially, slightly unstable and shifting. In spite of the significant movement downstream, only a small proportion of recovered mussels (7.1%) had moved beyond the initial plots to which they were allocated, and only two recoveries (0.3%) had moved a distance beyond 25 metres. Other than floods and receding waters over the shallows, presumably no other factor initiates a response in mussels to move far in a lifetime in the deep channel billabongs. In the deeper floodplain billabongs, however, deepwater anoxia might provide such a stimulus (section 6.5.3.1).

## 6.9 Discussion

The conspicuous dark rings that characterise the shells of Velesunio angasi in all freshwater environments of the Magela Creek were shown

to be annular in nature. By following the guidelines as set out in section 6.3.2 for distinguishing the annual growth rings these can be used to age mussels from the Magela Creek and presumably from other freshwater environments of the Region. The present study provides the first unequivocal evidence that rings on the shells of mussels from tropical environments may be used in age determinations. Indeed, the study provides the first substantiation that an Australian freshwater mussel species can be aged by this means.

Decreases in seasonal growth in mussels from waterbodies of the Magela Creek were attributed to food and oxygen depletions, and aestivation. Food depletions and aestivation were assumed to be the most obvious cause of growth cessation of mussels during the late Dry that resulted in the annual growth interruption bands of mussels in all environments. However, less conspicuous factors such as the channelling of energy into reproduction, increasing water temperatures, the fluctuating dynamics of algal populations and their effect upon oxygen conditions, and metal toxicity were also believed to be late Dry season causes of annular cessation rings. Late Dry season stresses were also found by Kenmuir (1980) and Dudgeon and Morton (1983) to retard mussel growth in the tropics. Thus, Tevesz and Carter's (1980a) suggestion that the silt load carried by Wet season floods might be the cause of growth cessation and annularity in the shell rings of tropical species of freshwater mussel may be incorrect and has yet to be demonstrated. Drought (McMichael, 1952) and low winter temperatures (Walker 1981b) are believed to be the main causes of growth cessation of mussels in other parts of Australia.

Despite some peculiarities in the growth of mussels at various life stages in Georgetown and Corndorl billabongs, and the unsuitability of growth data of young-of-year mussels, the von Bertalanffy growth equation proved to be an adequate model of growth description of mussel populations in the Magala Creek. This was confirmed by the conformity of growth data to linear Walford plots and by the close fit of the computed curves to the data. The von Bertalanffy growth equation has been used elsewhere to describe the growth of freshwater mussels (Kenmuir, 1980; Walker, 1981b; Dudgeon and Morton, 1983; McCuaig and Green, 1983), although it cannot be assumed that the model will always provide an adequate description of their growth (Green, 1980). Very few significant differences were found between growth rates of the two sexes and size for age data were therefore pooled for growth comparisons of mussels within and between waterbodies. If any trends were apparent they were towards a tendency for female mussels to grow slightly faster than males. However, in billabongs where females were underrepresented in the older age classes (section 6.7.1) the differences in growth rates were least obvious. Elsewhere female mussels may grow more quickly than males (Chamberlain, 1931; Haukioja and Hakala, 1978a) but similarly the differences are trivial.

Growth rates in relation to food availability were studied between mussel populations within and between waterbodies. Asymptotic size,  $L_{\infty}$ , of the von Bertalanffy growth equation, was used to compare growth between different populations. This parameter reflected growth rate differences throughout the lifespans of mussels in the populations compared, and has a stronger theoretical basis (over the parameter  $K$  of the equation) for use in the types of comparison in

which growth rates are related to food abundance (Beverton and Holt, 1957). Growth rates were found to vary quite considerably within billabongs. Within Mudginberri and Buffalo billabongs, significant correlations were found between growth rate and food availability. Growth rates of mussels decline with depth in Leichhardt billabong and similarly for the earlier age classes of mussels in Nankeen. Food and oxygen depletions with increasing depth may account for these reduced growth rates. Growth rates of older age classes of mussels in Nankeen billabong, however, are reduced in the shallower waters. This was believed to be associated with an interference to feeding of these later year stages, by wave-induced resuspension of the silty sediments during the Dry season. Growth rates varied widely between mussel populations of different waterbodies, being clearly correlated with mean food availability. The effect upon growth of mussels in waterbodies in which food abundance is low or the growing season short, is for maximum size to be attained relatively early in life and for little growth to occur in the older year classes. In more productive billabongs, or billabongs in which food is available over a relatively longer period of the year growth is discernible throughout most of the lifespan.

Very few studies have compared quantitatively, growth rate differences of freshwater mussels between different populations and in relation to possible environmental determinants. Haukioja and Hakala (1978a, 1979) recommended using the mean length of the third annulus in the shells of mussels, which have just passed their third winter, for growth comparisons between populations. Ghent et al. (1978) used mean height of mussels at the fifth annulus for growth comparisons of lake

populations of Anodonta grandis at different depths. Haukioja and Hakala (1979), however, admitted that the choice of a specific annulus for comparison was subjective and that the criterion would not be valid if the groups compared had clearly different final lengths.

Elsewhere, as for Velesuno angasi, growth rate differences of freshwater mussels within sites of streams (Brönmark and Malmqvist, 1982), over a depth gradient in lakes (Appendix 3), and between different sites of the same lake (Harman, 1970; Cvancara, 1972; Kenmuir, 1980) have been attributed at least partly to differences in food supply. This same factor has also been suggested as the cause of growth rate differences of mussels between different streams (Björk, 1962) and different lakes (Okland, 1963). Growth rates of mussels in the Magela Creek generally, were observed to increase downstream in accordance with increasing primary productivity in that direction. The phenomenon has been observed in streams of temperate regions too (Altnöder, 1926; Cvancara et al., 1978; Walker, 1981b). Cvancara and co-workers observed that a downstream increase in nutrients (and hence greater food availability) might also explain the observed growth rate differences of mussels. Walker thought, however, that increasing temperatures in the downstream direction were probably the cause of the observed growth disparities. The shallow water stunting of the older age classes at least, in the exposed environment of Nankeen billabong has also been a commonly observed phenomenon in exposed lake habitats elsewhere (Appendix 3). Brown et al. (1938) attributed the stunting effect to extra energy expended by mussels in maintaining their station in the unstable environments, and/or to food supply reductions that might prevail in exposed habitats.



Within sites, growth rates have been reported to decline with increasing mussel density (Kat, 1982) and with increasingly softer sediments of finer particle sizes (Brönmark and Malmqvist, 1982; Kat, 1982). Mussel densities of V. angasi were amongst the highest in the Magela Creek on the stony, clay sediments in Mudginberri and Buffalo billabongs (Table 5.4 and 5.5). At these sites, however, (site 5 in Mudginberri, Fig. 6.14 and adjacent to site 10 in Buffalo, Fig. 6.15) were recorded the highest growth rates of mussels in either billabong and high mussel densities therefore had no bearing upon reduced growth rates of the mussels. Kenmuir (1980) also found highest growth rates of mussels in Lake Kariba, amongst sites where densities were greatest. Higher growth rates of V. angasi were found upon the finer, silty and organic sediments of the two channel billabongs than food availability as measured by algal concentrations might suggest (section 6.4.3.1). The substrates possibly provide an additional detrital food supply for mussels here. While these sediments are fine and slightly unconsolidated, they obviously neither interfere with feeding nor cause mussels to expend constant energy towards retaining their position to any degree that would result in reduced growth rates. Thus, no competition for food resources was evident amongst mussels of the Magela Creek environments, nor was evidence found that growth rates were reduced over soft, silty sediments.

Apart from higher water temperatures, faster growth rates of freshwater mussels between different but neighbouring streams (Björk, 1962; Clarke, 1973) and lakes (Green, 1980) have otherwise been attributed to increasing water hardness. No measure of water hardness

between different waterbodies of the Magela Creek (Table 2.7), however, was correlated with growth rate of mussel populations in different waterbodies, as measured by asymptotic size,  $L_{\infty}$ , of the von Bertalanffy growth equation ( $P > 0.05$ ).

The broad aspects of the population structure of V. angasi studied in relation to habitat and environmental patterns in the Magela Creek were distribution of the sexes, and size and age distribution. No significant deviations were found in the proportions of the sexes between sites or different depths of billabongs in the Magela Creek that would suggest that the sexes were unevenly distributed. Cvancara (1972) similarly noted no apparent trend in sex ratio with depth in a lake population of freshwater mussels in North America.

In billabongs in which habitat related age structures were studied, size distributions closely mirrored the patterns evident in age distribution. Thus, both size and age of mussels were generally observed to increase with increasing depth in billabongs. In Georgetown billabong and the floodplain billabongs, this distributional pattern can be partly attributed to the recruitment of juveniles that was observed in the shallows. Presumably higher mortality in the shallows, and migration of older individuals to deeper waters to avoid high, Dry season water temperatures, exposure and increased predation, are further factors that modify the distributional patterns. In other studies, juveniles are generally noted to be more frequent in shallower waters than adults (section A2.1.3). Both Okland (1963) and Kenmuir (1980) similarly attributed the increase in size and age with depth, to the shallow water

recruitment of juveniles, and to the unstable environment of the shallows that results in higher mortality of mussels or that induces a migration of older mussels to deeper waters.

In Mudginberri and Buffalo billabongs, recruitment of juveniles is not necessarily confined to the shallows, but is apparently more influenced by Wet season flow patterns through the billabongs. The occurrence therefore of older mussels in the deeper waters of these billabongs is more difficult to explain, especially as extensive bottom areas of barely discernible slope lie between depth contours (Figs 2.8 and 2.9). The shallower waters of both billabongs, however, comprise mostly sandy sediments which are to some degree unstable during peak discharge events in the Magela Creek. Higher water temperatures can also be expected about the sediments of the shallower waters of these clean water billabongs, that either stimulate movement away from the shallows or perhaps increase the metabolic rates to such a degree as to reduce longevity of mussels here. Okland (1963) at least, thought the lack of younger mussels in the shallows of Lake Borrevann might partly be explained by selective mortality of faster growing individuals there. In both channel billabongs, moreover, mammalian predation is presumably higher in the shallows during the late Dry than elsewhere.

While older individuals are less common in the shallows, in the floodplain billabongs they are also less common at the greatest depths. Okland (1963) observed a similar phenomenon in Lake Borrevann in which the oldest mussels predominated at intermediate depths. As suggested by Okland, deepwater oxygen depletions may stimulate

movement of older mussels away from, and induce higher mortality of the older age classes in the deepest reaches. In Corndorl billabong, mean size of mussels was also observed to decline with depth. The deep waters of this billabong are seasonally deprived of oxygen, and harbour softer unconsolidated sediments than elsewhere. Older mussels may avoid or succumb in the deeper reaches of the billabong under these conditions. Both Fisher and Tevesz (1976) and Ghent *et al.* (1978) for example, explained the absence of mussels from the depths of certain lakes, by possible asphyxiation in the soft, unconsolidated sediments there. Kat (1982) at least, observed reduced growth rates of mussels on soft, muddy sediments. Both growth rates and mean age of mussels in the channel billabongs are relatively higher on the more silty and organic sediments. Obviously these are not so soft that mussels require a constant energy expenditure to maintain a footing or even asphyxiate, as is conceivable in the deeper waters of Corndorl billabong.

The age distributions of mussel populations between the different waterbodies were characterised by long-lived individuals, and various types of recruitment patterns were evident. Populations from Georgetown, the Magela Creek channel, and Mudginberri and Buffalo billabongs displayed reasonably regular decreases in numbers from juveniles to the oldest age groups, indicating regular year to year recruitment. This type of age distribution is noted in many freshwater mussel populations except for the absence of the very youngest age classes (van der Schalie and van der Schalie, 1963; Tudorancea and Florescu, 1968; Tudorancea and Gruia, 1968; Tudorancea, 1969, 1972; Magnin and Stanczykowska, 1971; Kenmuir, 1980). Thus,

in the Magela Creek, are represented some of the only known populations of mussels in which year to year variation in recruitment is minimal or exceedingly low. Invariably, the youngest age class is reported to be absent in studies of freshwater mussels. If the youngest age class was absent from any population in the Magela Creek, however, it was not because their habitat was so remote from that of adults, nor because of a specialised substrate requirement. The absence of young was attributed to inadequate sampling and poor conditions for survival of newly recruited mussels. The age distributions of populations from other billabongs, notably floodplain billabongs, were uneven and characterised by dominant year classes. This type of age distribution indicates irregular recruitment and is also common in freshwater mussel populations elsewhere (Negus, 1966; Haukioja and Hakala, 1978b; Walker, 1981b; and Strayer *et al.*, 1981). No terminal populations of mussels were found in the Magela Creek, and because the age distributions are skewed to the left, the populations in all waterbodies can be regarded as increasing and virile (Zaika, 1973).

An ecological basis for the variation in year to year recruitment in freshwater mussel populations has never previously been quantified in terms of important environmental factors. Discharge patterns, particularly during the late Wet season, accounted for significant proportions of the variation in year class strength of mussel populations in the floodplain billabongs of the Magela Creek. Higher Wet season discharge, particularly late in the Wet season, was argued to result in both enhanced larval production in adult female mussels and subsequent recruitment, and better survival of newly-recruited

mussels during the early Dry season. While drought was found to be a major factor adversely affecting recruitment of Alathyria jacksoni in the Murray River (Walker, 1981b), recruitment of Velesunio angasi in the floodplain billabongs, best resembles recruitment patterns of mussels in the Crapina-Jijila marshes. Tudorancea (1969, 1972) found that recruitment of Unio tumidus into the marshes was enhanced by high seasonal flooding of the Danube River. Strong year classes were traced back to years of high flooding in the Crapina populations.

Little evidence was found as to whether mussel populations in the Magela Creek could be regulated in a density dependent fashion. Both Kenmuir (1980) and Erönmark and Malmqvist (1982) thought that settlement of young mussels could be suppressed by adults when adult densities were high, and enhanced when adult densities were low. Recruitment onto the shallow and unstable, sandy transect in Georgetown was observed to be exceptionally high over the study period. Adult mussels are relatively scarcer in this region of the billabong than elsewhere and thus the age distribution might influence the recruitment patterns. However, the habitat requirements of the young may be exceptionally well met in the shallows of this transect, and recruitment might always be greater here.

The same causes of mortality of V. angasi in the Magela Creek have been reported or implicated for mussel populations elsewhere. These factors are predation (sections A2.1.2 and Appendix 3), drought and rapid subsidence of waters (Björk, 1962; Okland, 1963; Tudorancea, 1969, 1972; Walker, 1981b), flooding (section A2.1.3) and anoxia (Björk, 1962; Okland, 1963; Walker, 1981b; and section A2.1.3). In

broad comparisons between waterbodies, no evidence was found of growth selective or density dependent mortality. Comfort (1957) stated that slower growing molluscs tend to be longer-lived. Thus, Björk (1962), Okland (1963) and Haukioja and Hakala (1978a) considered that growth selective mortality operated on some freshwater mussel populations. Using asymptotic size ( $L_{\infty}$ ) from the von Bertalanffy growth equation as a measure of growth rate, and maximum age of mussels recorded from each waterbody, no significant correlation was found between growth rate and longevity ( $P > 0.05$ ) that might indicate growth selective mortality. Tudorancea and Gruia (1968) believed that high densities of Unio crassus in a site in the Nera River shortened their lifespan. Again, however, no correlation was found between mean density of mussels and longevity in waterbodies ( $P > 0.05$ ) that would suggest density dependent mortality. In fact the highest densities of mussels were recorded in the two channel billabongs, Mudginberri and Buffalo, where the longest-lived mussels in the Magela Creek were also found.

The proportions of female mussels in some billabongs of the Magela Creek were found to decline in the older year classes. This was also found by Tudorancea (1969) for the older ages of Unio tumidus, and might indicate differential mortality of females or sex transformations with age. Nevertheless, the occurrence of the phenomenon mainly in the floodplain billabongs suggests that the females, by virtue of the additional gill functions of larval brooding, are stressed by the low oxygen conditions of these environments.

The only significant events in the past that were believed to explain

mortality and low numbers in the age classes of the age distribution, were the effects of drought upon young of year mussels in Gulungul billabong. A correlation was found between year class strength of mussels, and presumed late Dry season drying up of the billabong. Juvenile V. angasi are less tolerant of dehydration than adults. Both Tudorancea (1969) and Walker (1981b) interpreted missing age classes in the age distributions of mussel populations to the devastating effects of past periods of high winds and wave action, and severe drought respectively. More recently, Bauer (1983) found correlations between mortality rates and organic pollution in populations of Margaritifera margaritifera in North Bavarian streams.

Indirect assessments of the factors underlying overall population mortality of mussels in the Magela Creek, however, were gained from estimation of age specific mortality rates for populations in three billabongs, in combination with knowledge of longevity of mussels in different populations. Mortality in the Georgetown mussel population was found to be more constant throughout the life span, apparently an exceedingly rare observation in animal populations (Odum, 1971). In both Mudginberri and Nankeen billabongs however, mortality at intermediate ages is minimal and even negligible, while mortality in the youngest and oldest age classes is highest. Negus (1966) also found mortality of Anodonta anatina in the Thames River to be negligible in the intermediate ages, while Green (1980) suggested that mortality in the youngest ages might be expected to be higher than in the intermediate ages.

Late Dry season stresses and increased mortality would be likely to be



severe enough in the shallow and unstable environment of Georgetown billabong to expect more or less constant mortality of mussels. Flood events, stranding and dehydration by receding waters, high water temperatures, high turbidities and mammalian predation might be expected to account for regular and constant loss of mussels from the billabong annually. At the other extreme, mussels in Mudginberri billabong suffer negligible mortality for a period of some ten years or so at intermediate ages, and the billabong is apparently a most favourable one for mussels. Water quality in the billabong remains unspoiled throughout most of the year and in addition to the relative depth of water left in the billabong at the end of the Dry season, contributes to a relatively stress-free environment. Most of the year classes in Nankeen billabong, however, are observed to decline from year to year. While water quality deteriorates in the late Dry season, the added stress of oxygen depletion during the Wet-Dry interchange is conceivably the factor that might contribute most to mortality of mussels in the billabong. Across all billabongs, a significant correlation was found between maximum age and mean dissolved oxygen concentrations, suggestive that mortality in the oldest age classes at least, is more influenced by dissolved oxygen than any other factor.

Longevity of V. angasi in the Magela Creek varied considerably between waterbodies, with determinations ranging from 11 to 35 years. While anoxia, and the ephemeral nature of other waterbodies may contribute to a shortened lifespan, other equitable environments such as those prevailing in Mudginberri and Buffalo billabongs are apparently most conducive to mussel development, and long lifespans may be expected.

Comparable light-shelled species in Europe, North America, Asia and Africa generally live from 10 to 15 years (Appendix 3). In Australia, the congener Velesunio ambiguus along the Murray River was estimated to live to 11 years while the heavier shelled mussel, Alathyria jacksoni was estimated to live to 29 years (Walker, 1981b). In suitable environments therefore, V. angasi lives to a greater age than comparable forms elsewhere. The genera Velesunio and Alathyria both belong to the subfamily Velesunioninae. Further studies on species in the subfamily may reveal that members are generally longer-lived, and may resemble more the longevities found for thicker shelled species in North America (Appendix 3). The wide range in longevities found in V. angasi for various waterbodies in one small catchment, nevertheless, exemplifies the importance of environmental quality upon mussel well-being. (The longevities themselves in fact, further accentuate how diverse and heterogeneous the various freshwater environments of the Magela Creek are in relation to water quality.) Thus, it is conceivable that a species with circumboreal distribution such as Margaritifera margaritifera should vary even more greatly with respect to the maximum ages attained. Criticism of the reports of the extreme ages attained by this species therefore (Thompson et al., 1980; Dudgeon and Morton, 1983), may not be entirely valid because they did not fully consider the environmental and phylogenetic influences on longevity.

Mussel movements over a lifetime in selected environments of the Magela Creek were likely to be very limited in the absence of sufficient stimuli. In an equitable, stress-free environment where Wet season stream velocities are not particularly strong, such as in

Buffalo billabong, this is probably to be expected (Evermann and Clark, 1917). Thus in Buffalo, only 7.1% of mussels were observed to have moved beyond the 506 m<sup>2</sup> quadrats to which they were allocated one year previously. Most of the movements appeared to be associated with slight displacement downstream from Wet season flood events. Significant movements, apparently regular and seasonal, were observed over a shallow, sandy transect in Georgetown billabong. The stimulus for mussels here to move onto the shallow, seasonally inundated banks during the Wet season may arise for a number of reasons: avoidance of the unstable, and shifting sandy sediment in the centre of the transect; better feeding conditions at the edges of the billabong; and to increase the chances of parasitizing the host fishes with the glochidial larvae. Elsewhere, movement of mussels over unstable sediments and in response to rising water levels in lotic environments has also been observed (Coker *et al.*, 1921; Björk, 1962; Kat, 1982; Salmon and Green, 1983). Similarly, both seasonal movements related to feeding (Tudorancea, 1972) and reproduction (Ellis, 1931; Yokley, 1972; Brönmark and Malmqvist, 1982), have been noted in various other freshwater mussel populations. In both Georgetown and Buffalo billabongs, mussels were observed to retreat to deeper waters in response to receding water levels over the Dry season. Again, this has been a commonly observed phenomenon in other mussel populations (Coker *et al.*, 1921; Björk, 1962; Tudorancea, 1972; Fuller, 1974; Kenmuir, 1980; Salmon and Green, 1983), and is a response attributed to avoidance of dehydration, high water temperatures and increased predation. The seasonal migrations of mussels in Georgetown billabong most resembled the movements of mussels in the Crapina-Jijila marshes; migrations in the marshes occur onto seasonally inundated floodplains

for feeding and reproduction; and mussels retreat into deeper waters as the waters recede during the summer (Tudorancea, 1972). Thus, rising and falling water levels in shallow water environments, significant water movement, and conceivably anoxia in the floodplain billabongs are possible stimuli that initiate responses in V. angasi to movement in environments of the Magela Creek.

Finally, in addition to the indicator role that distributional information about V. angasi can offer (i.e., of the flow regime in waterways and the dissolved oxygen environment in waterbodies, section 5.5), further roles can be advocated with knowledge of the population dynamics of the mussel in the Magela Creek. For example, there have been no previous attempts in studies of freshwater mussel populations to demonstrate quantitatively, temporal variations in recruitment patterns related to environment; to calculate age specific mortalities for the entire age distribution in a relatively undisturbed environment; nor to show significant correlations between growth rate and size distribution, and algal productivity. V. angasi therefore, may be used as an indicator of environmental impact, and of past and present environments much as suggested by Tevesz and Carter (1980a). In association with distributional data, it is conceivable that recruitment patterns and mortality estimates that differ significantly from baseline data collected in the present study, could indicate environmental change in the Magela Creek brought about by anthropogenic activities such as pollution.

While distributional information about V. angasi indicates the long-term oxygen status of freshwaters (section 5.5), growth rate data

are clearly correlated with algal production and therefore may indicate the trophic status of a waterbody. Because of the correlation between growth rate and water temperatures (e.g. Negus, 1966), both freshwater and marine mussels in temperate environments have already been suggested as useful palaeothermometers, indicators of thermal pollution or in interpreting past and present climates at sites uninhabited by man (Tevesz and Carter, 1980a; McCuaig and Green, 1983; Jones, 1983). Similarly, it is conceivable that throughout the Region and indeed perhaps throughout its wider geographical range in tropical northern Australia, analysis of the size distribution and growth rates of populations of V. angasi will assist in the knowledge of limnology of both past and present environments. Oxygen relations and trophic status of freshwaters are fundamentally important limnological parameters, and a good understanding of both relationships may be gained from data on distribution and abundance, and size and growth rate data of mussels respectively. Thus V. angasi may prove a useful 'palaeotrophic' indicator or may be useful in interpreting the trophic status of tropical freshwaters previously unstudied. Additionally, in terms of pollution, growth rate data that exceed the rates calculated from baseline data might indicate forms of mild organic pollution in waterways. Such uses of freshwater mussels have not previously been suggested.